The
American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

Arthur L. Schipper, *Editor*

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Gross Anatomy of the Wing Muscles in the Family Corvidae

George E. Hudson and Patricia J. Lanzillotti
State College of Washington, Pullman

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INTRODUCTION

The purpose of this investigation was to prepare a fully described and illustrated account of the musculature of the pectoral appendage in a common species of bird. The crow and raven were selected as types that are easily available over much of the earth. While preparing this paper it was considered expedient to make a comparative examination of as many genera as possible to determine what modifications might be expected within the family Corvidae. It is hoped that this preliminary work will help to stabilize the muscle nomenclature and serve as a basis for detailed comparisons yet to be made for other orders and families of birds.

Gadow and Selenka (1891) were the first to undertake a broad comparative study of the musculature in different families and orders and to bring together in one work the complete synonymy of names used for the various

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muscles. We have adopted the terminology of Gadow and Selenka except in a few cases where this does not appear to be expedient. Muscle names have been brought into conformity with the BNA where the homologies appear to be firmly established. The terminology of Gadow and Selenka is fully latin-ized and this is essential if the names of bird muscles are to be accepted on a universal basis.

Shufeldt (1890) was the first American to make an important study of the musculature in any bird. In many cases he invented names for muscles during a time when he did not have access to the literature, although in footnotes he gave the synonymy of muscle names as listed by Gadow and Selenka. He did not find the pectoralis propatagialis, abductor indicis, expansor secundari-orum, and the ulnimetacarpalis dorsalis in the raven, although they are present in all corvids we have examined. He also failed to differentiate between the flexor carpi ulnaris and the flexor digitorum sublimis. His description of the flexor digitorum sublimis makes it quite apparent that he did not find any such muscle. We have made a careful examination of many specimens to try to find muscles described by Shufeldt as the flexor minimi digiti brevis, abduc-tor minimi digiti and flexor metacarpi brevis, and we have reached the definite conclusion that no such muscles are present and further that he was referring to ligaments. Shufeldt's work has served a useful purpose in stimulating inter-est in the musculature of birds and has made the important synonymies of Gadow and Selenka widely available.

The work of Fürbringer (1902) is probably the most thorough investiga-tion yet made of the anatomy of any region in birds. His study of the shoulder involved extensive comparisons of many different types and his no-menclature followed very closely that of Gadow and Selenka.

Marshall (1905, 1906) studied the wing muscles in the poor-will (*Phalaenoptilis nuttallii*), the road-runner (*Geococcyx californianus*) and the horned owl (*Bubo virginianus*). This is the first comparative study made in America of all the muscles of the bird wing. She used the terminology of Gadow and Selenka, and, for the most part, identified the wing muscles cor-rectly, but there are a few discrepancies; for example, the muscle she designates with the letter "A" appears to represent the distal head of the extensor indicis longus and the one labeled "D" the extensor pollicis brevis.

Leach (1914) made a detailed comparison of the muscles of the wing and leg in *Corvus* with the bell magpies. He found that in the latter the posterior head of the latissimus dorsi is absent. On the basis of this and other consider-ations he concluded that the bell magpies should be in a separate family, the Streperidae (Cracticidae). We have examined a specimen of *Strepera gracu-lina* and confirmed the fact that the latissimus dorsi posterior is absent.

In a study of the development of the wrist and hand region in *Anser*, Schestakowa (1928) refers briefly to muscles in the area.

Burt (1930) considered the muscles of the wing in the woodpeckers using, for the most part, the terminology of Shufeldt. Exceptions to this have been noted in our list of synonymies. Burt found two parts to the rhomboideus profundus and called them the "anticosublimis" and "posticoprofundus." He points out the absence of the latissimus dorsi posterior in the pileated wood-pecker (*Dryocopus*). He describes a flexor minimi digiti brevis and a flexor

metacarpi brevis following Shufeldt. The first of these we consider as belonging to the distal end of the flexor digiti III and the latter is a ligament. Burt overlooked the ulnimetacarpalis dorsalis and extensor pollicis brevis which we find to be present in *Dryocopus* and *Colaptes*.

Holmgren (1933) studied the development of the bones of the wing in several groups of birds and concluded that the three digits represent the second, third and fourth.

Howell (1937) studied the homologies of the shoulder muscles in the domestic fowl (*Gallus*) on the basis of innervations and other considerations and compared them with *Iguana* and the Mammalia.

Ashley (1941) briefly considered muscle attachments on the humerus in the Corvidae, together with the innervations of the muscles involved. His muscle terminology is a mixture of names used by Shufeldt, Gadow and Selenka, and Howell.

Fisher (1946) made a detailed comparison of the wing muscles in four genera of Cathartidae. The muscle names used in many cases follow those of Gadow and Selenka, and Fürbringer, but in some the names of Shufeldt and Howell are used. The muscle called "proscapulohumeralis brevis" represents the scapulohumeralis anterior, which in the vultures is very small. He does not mention the expansor secundariorum which we have found in *Cathartes* and *Coragyps*, although in these birds it is largely ligamentous. This important work includes the innervations of the various muscles and gives considerable attention to the variations in function in the different genera.

Material and Methods

Specimens for dissection and celloidin cross sections were prepared essentially as described in a previous paper (Hudson, 1937). Complete dissections were made and every muscle studied on at least one wing of the specimens listed below. In many cases points of particular interest were examined on the opposite side.

Corvus brachyrhynchos	±40	*Garrulus glandarius*	1
C. corax	3	*Cyanocorax chrysops*	1
Nucifraga columbiana	2	*Psilorhinus morio*	2
Cyanocitta stelleri	2	*Gymnorhinus cyanocephalus*	1
Pica pica	2	*Kitta chinensis*	1
Perisoreus canadensis	2	*Cissolopha beecheyi*	1
Aphelocoma·c. coerulescens	2	*C. yucatanica*	1
A. c. californica	2	*Calocitta formosa*	1
A. c. insularis	1	*Cyanolyca mirabilis*	1
A. ultramarina	2		

In order to avoid confusion axes mentioned in the descriptions refer to the extended wing without regard to phylogenetic considerations.

Digits of the hand are considered to represent numbers one, two and three, rather than two, three and four, as given by some authors.

ABBREVIATIONS

Abbreviations for wing muscles are given under the descriptions of those concerned. In addition the following are used in the text or figures.

Cos. ster.—M. costi sternalis

Cos. ster. ant.—M. costi sternalis anterior

Int. cos. ext. and int.—Mm. intercostales externus and internus

L. col. ant.—M. longus colli anticus

Lev. cos.—Mm. levatores costarum

Ob. ab. ext.—M. obliquus abdominis externus

Sca.—M. scalenus

The following abbreviations are used for skeletal structures.

Cerv.—Cervical

Tho.—Thoracic

Vert.—Vertebra

Cris. ster.—Crista sterni

Mem. ster. cor. cl.—Membrana sterno-coraco-clavicularis

Os hum. scap.—Os humeroscapulare

Cris. lat. hum.—Crista lateralis humeri

Cap. hum.—Caput humeri

Tuber. lat. hum.—Tuberculum laterale humeri

Tuber. med. hum.—Tuberculum mediale humeri

Cris. med. hum.—Crista medialis humeri

For. pneu.—Foramen pneumaticum

Epicon. lat. hum.—Epicondylus lateralis humeri

Epicon. med. hum.—Epicondylus medialis humeri

Corp. hum.—Corpus humeri

Rad.—Radius

Tuber. rad.—Tuberositas radii

Corp. rad.—Corpus radii

Ul.—Ulna

Proc. coron.—Processus coronoideus

Corp. ul.—Corpus ulnae

Meta.—Metacarpal

Tuber. mus. meta.—Tuberositas muscularis metacarpi

Phal.—Phalanx

Dig. I—Digit I (Pollex)

Dig. II—Digit II (Index)

Dig. III—Digit III (Medius)

REVIEW OF THE MUSCLES OF THE PECTORAL APPENDAGE
M. latissimus dorsi (Lat. dor.)

1890 Shufeldt	1891 Gadow and Selenka	1902 Fürbringer	1937 Howell	1946 Fisher
52. *Latissimus dorsi,* p. 81.	68. *Latissimus dorsi,* p. 226.	13. *Latissimus dorsi (inkl. Teres major),* p. 480.	*Latissimus dorsi,* p. 369.	*Latissimus dorsi,* p. 581.
Anterior slip p. 82.	I. Anterior part, p. 227.	a. *Latissimus dorsi anterior (inkl. Teres major),* p. 481.	Anterior part.	*Pars anterior.*
Posterior slip p. 82.	II. Posterior part, p. 227.	b. *Latissimus dorsi posterior* p. 487.	Posterior part.	*Pars posterior.*
	III. *Pars meta-patagialis,* p. 228.	c. *Latissimus dorsi meta-patagialis and latissimus dorsi dorso-cutaneus,* p. 496.		Dermal component.

Description (for the crow and raven).—This superficial muscle consists of two distinct parts, one anterior, the other posterior.

LATISSIMUS DORSI ANTERIOR (Lat. dor. ant.; figs. 1-3)

This thin flat sheet arises mostly tendinous from the spinous processes of the last cervical vertebra, the first thoracic vertebra and the anterior tip of the second and the ligaments between them (figs. 11, 15). It passes antero-laterally, and a little more than half-way its course disappears between the scapular and humeral heads of the triceps. It inserts fleshy on the upper surface of the distal portion of the Cris. lat. hum., adjacent to the insertion of the Delt. maj. (figs. 11, 16a).

LATISSIMUS DORSI POSTERIOR (Lat. dor. post.; figs. 1-3)

This is also a thin flat muscle and is somewhat wider than the preceding. It arises directly behind the Lat. dor. ant. by a thin, tendinous sheet from the spinous processes of the posterior part of the second, the third and the fourth thoracic vertebrae (figs. 11, 15). About four-fifths of the way toward the insertion it passes beneath the Lat. dor. ant. and inserts by a short, narrow tendon on the posterior surface of the humerus, a short distance behind the postero-proximal edge of the insertion of the Lat. dor. ant. The insertion of
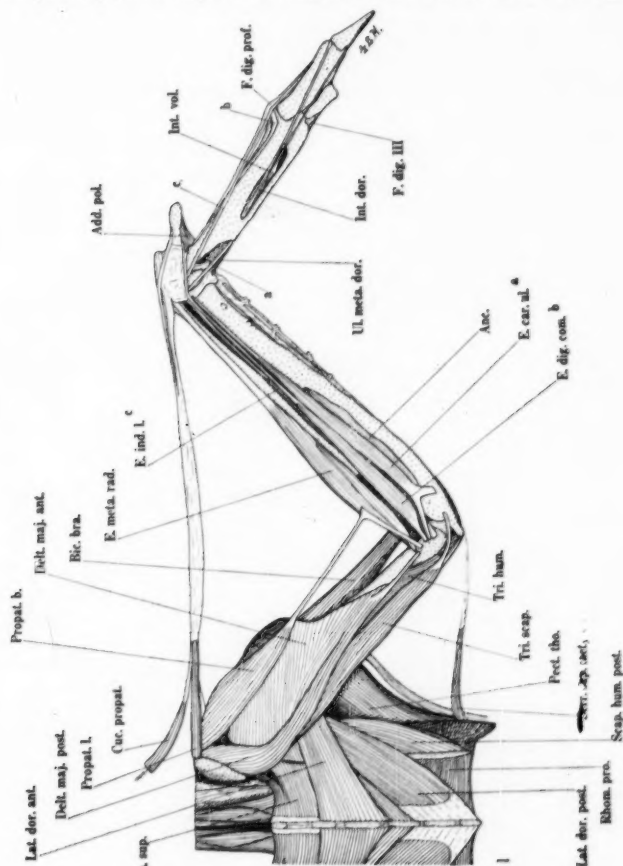
Fig. 1.—Crow (*Corvus brachyrhynchos*). Dorsal view of wing with skin and feathers removed. ×.6.

the Lat. dor. post. perforates the origin of the Tri. hum. near the proximal end of that muscle (fig. 16a).

Action.—The Lat. dor. ant. and post. tend to rotate the humerus backward against the scapula. Pretchtl (Gadow and Selenka, 1891, p. 229) has suggested that it is chiefly the action of this muscle that gives the body of the bird its horizontal position in flight.

Innervation.—Branches of the *Nn. brachiales superiores,* Gadow and Selenka, 1891, p. 229; Fürbringer, 1902, p. 335. *N. thoracodorsalis,* Howell, 1937, p. 369. *N. brachialis longus superior,* Fisher, 1946, p. 581.

Comparison.—The space between the bellies of the Lat. dor. ant. and post. is narrow in *Corvus.* In all other forms studied this space is about as wide as, or wider than, the width of the belly of the Lat. dor. post. This difference in spacing of the two heads is due to variations in the extent of the origins.

The tendon of the Lat. dor. post. generally has a more or less distinct tendinous con-
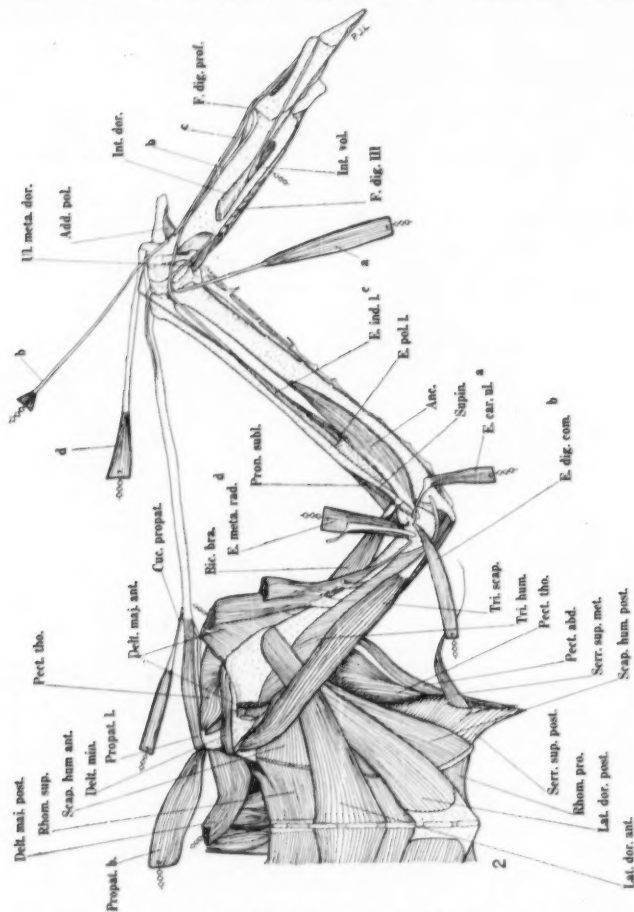
Fig. 2.—Crow, as in fig. 1, but with Propat. b., Delt. maj., E. meta. rad.,
E. dig. com. and E. car. ul. displaced. ×.6.

nection with the ventral side of the belly of the Delt. maj. ant. This is best developed in *Gymnorhinus, Cyanocorax, Cissolopha yucatanica* and *Calocitta.*

In many birds, such as the falcons, there is a *Latissimus dorsi metapatagialis* (Lat. dor. met.) which arises adjacent to the posterior margin of the Lat. dor. post. and inserts into the posterior end of the humeral feather tract, where it is closely associated with the Serr. sup. met. (fig. 33). When present the Lat. dor. met. helps to tense the metapatagial membrane. This muscle is absent in the Corvidae.

M. RHOMBOIDEUS SUPERFICIALIS (Rhom. sup.)

Trapezius, No. 53, Shufeldt, 1890, p. 82. *Rhomboideus superficialis,* No. 65a, Gadow and Selenka, 1891, p. 217. *Rhomboideus superficialis,* No. 2, Fürbringer, 1902, p. 372. *Rhomb. superf.,* Howell, 1937, p. 369; Fig. 3c, p. 373. *Rhomboideus superficialis,* Fisher, 1946, p. 582.

Description (for the crow and raven; figs. 1-3).—A thin flat muscle, arising by a tendinous sheet from the spinous processes of the last two cervical, the first two thoracic vertebrae and the anterior half or more of the third (figs. 11, 15). The fibers are directed antero-laterally to the fleshy insertion on about the anterior two-thirds of the dorso-medial surface of the shaft of the scapula (figs. 11, 14). A short distance from the anterior end of the muscle the insertion is interrupted by blood vessels and nerves emerging from the thorax. Anteriorly the Rhom. sup. is visible superficially but posteriorly is covered extensively by the two bellies of the Lat. dor.

Action.—Tends to draw the scapula toward the vertebral column and somewhat toward the rear.

Innervation.—Through the *Nn. thoracici superiores,* Gadow and Selenka, 1891, p. 218; Fürbringer, 1902, p. 332. *Nn. thoracales posteriores,* Howell, 1937, p. 366. Posterior cervical spinal nerves, Fisher, 1946, p. 582.

Comparison.—Slight differences in this muscle were noted as follows:

Origin extends caudad onto third thoracic vertebra	Origin not clearly connected with third thoracic vertebra
Perisoreus	*Pica*
Cyanocitta	*Nucifraga*
Aphelocoma	*Cyanocorax*
Garrulus	*Psilorhinus* (one specimen)
Corvus	
Gymnorhinus	
Psilorhinus (one specimen)	
Kitta	
Cissolopha	
Calocitta	
Cyanolyca	

Many species show a small slip at the anterior end of the insertion, separated from the main belly by a small bundle of nerves.

Anterior slip evident	Anterior slip not observed
Perisoreus	*Cyanocitta* (one specimen)
Cyanocitta (one specimen)	*Aphelocoma c. coerulescens*
Aphelocoma coerulescens insularis	*A. c. californica* (one specimen)
A. c. californica (one specimen)	*Pica*
A. ultramarina	*Kitta*
Garrulus	*Cissolopha yucatanica*
Corvus	
Gymnorhinus	
Nucifraga	
Cyanocorax	
Psilorhinus	
Cissolopha beecheyi	
Calocitta	
Cyanolyca	

M. RHOMBOIDEUS PROFUNDUS (Rhom. pro.)

Rhomboideus, No. 54, Shufeldt, 1890, p. 84. *Rhomboideus profundus*, No. 65b, Gadow and Selenka, 1891, p. 218. *Rhomboides profundus*, No. 3, Fürbringer, 1902, p. 380. *Rhomboideus posticoprofundus; Rhomboideus anticosublimis*, Burt, 1930, p. 486. *Rhomb. prof.*, Howell, 1937, p. 369; fig. 3c, p. 373. *Rhomboideus profundus*, Fisher, 1946, p. 582.

Description (for the crow and raven; figs. 1-4).—A thin, flat muscle, arising partly fleshy from the spinous processes of the last cervical and anterior four thoracic vertebrae (figs. 11, 15). The insertion is fleshy on about the posterior two-fifths of the dorso-medial border of the shaft of the scapula (figs. 11, 14). Anteriorly the fibers are directed postero-laterally but at the posterior end they pass almost directly laterally. The Rhom.
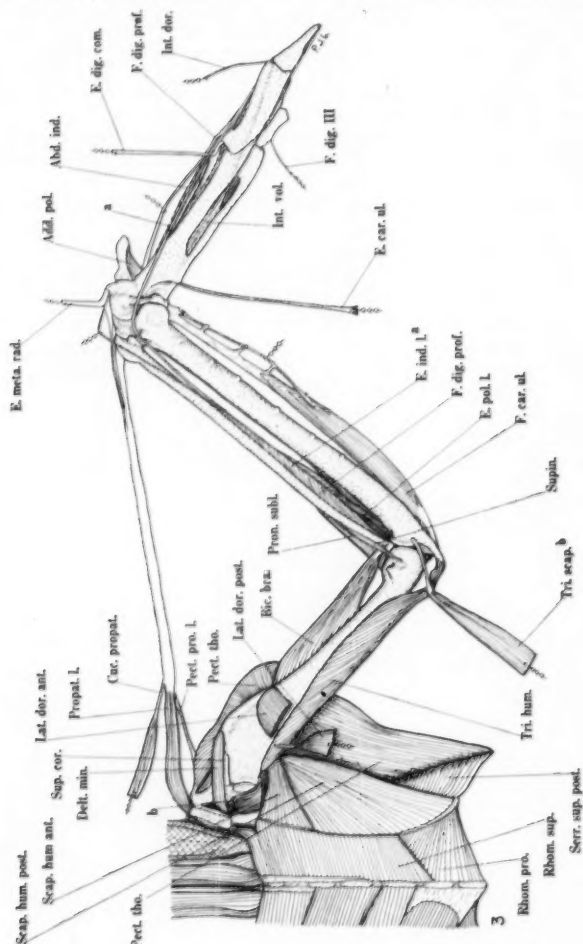
Fig. 3.—Crow, as in fig. 1, but with Lat. dor., Propat. b., Delt. maj., Tri. scap., E. meta. rad., E. dig. com., E. car. ul., Int. dor., and F. dig. III wholly or partly removed. x.6.

pro. is mostly covered superficially by the Rhom. sup. in its anterior half and by the Lat. dor. post. in its posterior half. However, a small triangular section is visible superficially on the medial side of the posterior end of the scapula. The posterior margin of the Rhom. pro. is overlapped slightly by the antero-proximal edge of the belly of the sartorius.

Action.—Tends to pull the scapula toward the vertebral column.

Innervation.—Through the *Nn. thoracici superiores,* Gadow and Selenka, 1891, p. 220; Fürbringer, 1902, p. 332. *Nn. thoracales posteriores,* Howell, 1937, p. 366. Posterior cervical spinal nerves, Fisher, 1946, p. 582.

Comparison.—Very little variation was noted in this muscle. In one specimen of *Psilorhinus,* in *Cyanocorax* and *Cissolopha yucatanica,* the anterior edge of the origin extends craniad a little in front of the spinous process of the fourteenth cervical vertebra. In all other specimens the origin does not reach this far anteriorly.

M. SERRATUS PROFUNDUS (Serr. pro.)

Levator scapulae, No. 63, and *Serratus parvus anticus,* No. 66, Shufeldt, 1890, pp. 98 and 104. *Serratus profundus,* No. 66a, Gadow and Selenka, 1891, p. 220. *Serratus profundus,* No. 5, Fürbringer, 1902, p. 404. *Levator scapulae,* Burt, 1930, p. 489. *Serratus profundus,* Fisher, 1946, p. 588.

Description (for the crow and raven; figs. 4, 8, 9).—This muscle consists of three fleshy slips arranged in a linear series. The stronger anterior slip arises from the transverse processes of the 12th and 13th cervical vertebrae; the middle slip from a small area on the outer surface of the last cervical rib; the posterior slip from a small area on the outer surface of the first thoracic rib (fig. 15). All three slips extend postero-dorsally to a common fleshy insertion on the medial surface of the scapula (fig. 14).

From the dorsal side the Serr. pro. is exposed by removing the Lat. dor. and Mm. rhom. and deflecting the scapula laterally.

Action.—Tends to draw the blade of the scapula antero-ventrally.

Innervation.—Through the *Nn. thoracici superiores,* Gadow and Selenka, 1891, p. 221; Fürbringer, 1902, p. 332. *Nn. thoracales posteriores,* Howell, 1937, p. 366. A branch of the *N. brachialis superior,* Fisher, 1946, p. 588.

Comparison.—The three slips of this muscle are clearly evident in practically all specimens although they vary somewhat in size and shape. In two specimens of *Aphelocoma coerulescens* the posterior slip was absent and in another specimen it was present but very small.

M. SERRATUS SUPERFICIALIS ANTERIOR (Serr. sup. ant.)

Thoraco-scapularis, No. 64, Shufeldt, 1890, p. 99. *Serratus superficialis s. thoraciscapularis:* I. *Pars anterior,* No. 66b, Gadow and Selenka, 1891, p. 221. *Serratus superficialis anterior,* No. 4a, Fürbringer, 1902, p. 387. *Anterior serratus,* Howell, 1937, p. 369. *Serratus anterior,* Fisher, 1946, p. 588.

Description (for the crow and raven; figs. 4, 8, 9).—Consists of two parts, a small anterior slip, and a much larger posterior one. The two are separable only near their origins. The small anterior slip arises fleshy from the lower end of the last cervical rib on its outer surface. The posterior slip arises fleshy from the ventro-lateral surface of the uncinate process and from the adjacent shaft of the first thoracic rib (fig. 15).

The common belly extends antero-dorsally forming a flat tendinous sheet which inserts partly on the ventral border of the belly of the P. int. M. subscp.; however, the main part of the tendon passes between the two heads of the Subscp. and inserts on the ventro-lateral border of the scapula about one-third the distance from the glenoid fossa to the posterior end (figs. 13, 14).

Laterally the Serr. sup. ant. is exposed by removal of the Pect. tho., severing the axillary nerves and blood vessels and rotating the humerus antero-dorsad.

Action.—Tends to draw the scapular blade ventrally and caudally and to move the ribs involved anteriorly and laterally.

Innervation.—Through the *Nn. thoracici superiores,* Gadow and Selenka, 1891, p. 224; Fürbringer, 1902, p. 333. Branches of Nn. 14, 15, 16, Howell, 1937, p. 369. A branch of the *N. brachialis superior,* Fisher, 1946, p. 588.

Comparison.—The only conspicuous difference noted in this muscle was the relative size of the anterior and posterior slips.

Anterior slip small	Anterior slip intermediate	Anterior slip at least one-half size of posterior slip
Pica	*Gymnorhinus*	*Perisoreus*
Garrulus	*Cissolopha*	*Cyanocitta*
Corvus		*Aphelocoma*
Psilorhinus (one		*Nucifraga*
specimen)		*Cyanocorax*
Kitta		*Cyanolyca*

In *Calocitta* (one side only) and in one specimen of *Psilorhinus* (one side only) the belly was undivided.
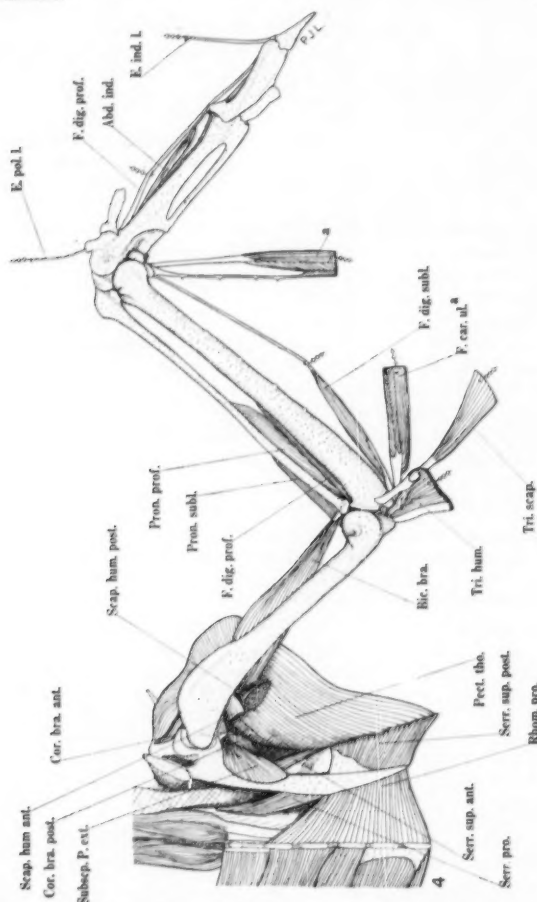
Fig. 4.—Crow, as in fig. 3, but with Rhom. sup., Cuc. propat., Pect. pro. l., Propat. l., Delt. min., Sup. cor., Scap. hum. ant. and post., Tri. hum., Supin., E. ind. l., E. pol. l., Add. pol. and Int. vol. wholly or partly removed. The F. car. ul. and F. dig. subl. have been displaced. ×.6.

M. SERRATUS SUPERFICIALIS POSTERIOR (Serr. sup. post.)

Serratus magnus anticus, No. 59, Shufeldt, 1890, p. 92. *Serratus superficialis s. thoraci-scapularis: II. Pars. posterior,* No. 66b, Gadow and Selenka, 1891, p. 221. *Serratus superficialis posterior,* No. 4b, Fürbringer, 1902, p. 392. *Posterior serratus,* Howell, 1937, p. 369. *Serratus posterior,* Fisher, 1946, p. 586.

Description (for the crow and raven; figs. 2-4, 8, 9).—This muscle is much larger than the Serr. sup. ant. and consists of three indistinct and closely fused fasciculi which arise from small areas on the lateral surface of the uncinate process of the first and the shafts of the second, third and fourth thoracic ribs just below the uncinate processes (fig. 15). Origin from the second rib is partly fleshy, that from the third and fourth is mainly tendinous. The large flat belly extends dorsally to the insertion on the ventro-lateral edge of about the posterior one-third of the shaft of the scapula (fig. 14). Anteriorly the insertion is by a thin tendinous sheet but the posterior part is comparatively thick and fleshy.

Action.—Tends to draw the blade of the scapula ventrally.

Innervation.—Branches of the *Nn. thoracici superiores,* Gadow and Selenka, 1891, p. 224; Fürbringer, 1902, p. 333. Branches of Nn. 14, 15, 16, Howell, 1937, p. 369. Branches of the *N. brachialis longus superior,* Fisher, 1946, p. 586.

Comparison.—The following variations were noted:

No connection with the uncinate process of the first thoracic rib	Origin includes the uncinate process of the first thoracic rib
Perisoreus	*Cyanocitta* (right side of one specimen)
Cyanocitta (one specimen and left side of another)	*Aphelocoma c. coerulescens* (one specimen)
Aphelocoma c. coerulescens (one specimen)	*A. c. insularis*
	A. c. californica
A. ultramarina (one specimen)	*A. ultramarina* (one specimen)
Psilorhinus	*Pica*
Kitta	*Garrulus*
Cissolopha	*Corvus*
Calocitta	*Gymnorhinus*
Cyanolyca	*Nucifraga*
	Cyanocorax

In *Corvus, Gymnorhinus, Nucifraga, Psilorhinus, Cissolopha* and *Calocitta* the origin from the fourth thoracic rib is mainly tendinous instead of mainly fleshy as in other forms.

M. SERRATUS SUPERFICIALIS METAPATAGIALIS (Serr. sup. met.)

Dermo-ulnaris, No. 11, Shufeldt, 1890, p. 12. *Serratus superficialis s. thoraci-scapularis: III. Pars metapatagialis,* No. 66b, Gadow and Selenka, 1891, p. 221. *Serratus superficialis metapatagialis,* No. 4c, Fürbringer, 1902, p. 398. *Serratus metapatagii,* Howell, 1937, p. 369. *Serratus metapatag.,* Fisher, 1946, table 19, p. 609.

Description (for the crow and raven; figs. 1, 5, 8).—This small, flat muscle slip arises partly fleshy from a small and vaguely-defined area on the lateral surfaces of the third and fourth thoracic ribs, adjacent to the lower edge of the Serr. sup. post. (fig. 15). The belly becomes narrower as it passes out into the metapatagial skin fold where it connects with a weak and indefinite elastic tendon which usually disappears as it approaches the elbow joint. In some specimens the belly of the Serr. sup. met. is somewhat attached to the posterior end of the humeral feather tract.

Action.—Tenses the metapatagial membrane.

Innervation.—Branches of the *Nn. thoracici superiores,* Gadow and Selenka, 1891, p. 224; Fürbringer, 1902, p. 333. Branches of Nn. 14, 15, 16, Howell, 1937, p. 369.

Comparison.—No differences worth mentioning were noted in this muscle.

M. SCAPULOHUMERALIS ANTERIOR (Scap. hum. ant.)

Supraspinatus, No. 57, Shufeldt, 1890, p. 88. *Scapuli-humeralis anterior,* No. 71a, Gadow and Selenka, 1891, p. 235. *Scapulo-humeralis anterior,* No. 15a, Fürbringer, 1902,

p. 544. *Proscapulohumeralis*, Howell, 1937, p. 370. *Proscapulohumeralis brevis*, Fisher, 1946, p. 587.

Description (for the crow and raven; figs. 2, 3).—A small, flat muscle which is exposed upon removal of the Delt. maj. post., the scapular head of the triceps and the Lat. dor. ant. It is fleshy throughout and lies directly behind the shoulder joint, being attached along its anterior border to the joint capsule. It arises from about the anterior one-fourth of the dorso-lateral surface of the shaft of the scapula (figs. 11, 13) and inserts on the posterior side of the *Caput humeri*, just distal to the For. pneu. (figs. 12, 16a). At its insertion the Scap. hum. ant. divides the proximal end of the Tri. hum.

Action.—Tends to move the humerus posteriorly toward the body.

Innervation.—A branch of the *Nn. brachiales superiores*, Gadow and Selenka, 1891, p. 237; Fürbringer, 1902, p. 334. *Nn. axillares*, Howell, 1937, p. 366. *N. brachialis longus superior*, Fisher, 1946, p. 584.

Comparison.—In *Garrulus* the origin is from about the anterior one-sixth of the blade of the scapula; in all others the origin is from about the anterior one-fourth or slightly less.

Fig. 5.—Crow. Ventral view of wing with skin removed. ×.6.

M. SCAPULOHUMERALIS POSTERIOR (Scap. hum. post.)

Teres et infraspinatus, No. 58, Shufeldt, 1890, p. 90. *Scapuli-humeralis posterior*, No. 71b, Gadow and Selenka, 1891, p. 236. *Scapulo-humeralis posterior*, No. 15b, Fürbringer, 1902, p. 549. *Dorsalis scapulae*, Howell, 1937, p. 369. *Dorsalis scapulae*, Fisher, 1946, p. 584.

Description (for the crow and raven); figs. 1-4, 6-8).—A large, flat, triangular muscle lying immediately behind the Scap. hum. ant. The origin is fleshy from a large area on the dorso-lateral surface of about the posterior three-fourths of the shaft of the scapula (figs. 11, 13). Distally the fibers converge to the strong and partly fleshy insertion on the postero-ventral margin of the *Caput humeri*, below and slightly distal to the For. pneu. and adjacent to the ventro-proximal end of the Tri. hum. (fig. 16a).

From the dorsal side most of the belly is exposed by removing both parts of the Lat. dor.

Action.—Draws the brachium posteriorly, at the same time rotating the posterior edge of the wing dorsally.

Innervation.—Branches of the *Nn. brachiales superiores*, Gadow and Selenka, 1891, p. 237; Fürbringer, 1902, p. 334. *Nn. axillares*, Howell, 1937, p. 366. A branch of the *N. brachialis longus superior*, Fisher, 1946, p. 586.

Comparison.—In *Garrulus* the origin is from about the posterior five-sixths of the scapular blade. In all others examined the origin is from about the posterior three-fourths or slightly more.

M. PECTORALIS

1890 Shufeldt	1891 Gadow and Selenka	1902 Fürbringer	1937 Howell	1946 Fisher
	73. *Pectoralis*, p. 241.	7. *Pectoralis*, p. 417.		
49. *Pectoralis major*, p. 69	I. *Pars thoracica*, p. 242.	(a) *Pectoralis thoracicus*, p. 418.	*Pectoralis superficialis*, p. 372.	*Pectoralis superficialis*, p. 577.
	II. *Pars propatagialis*, p. 245.	(b) *Pectoralis propatagialis*, p. 429.		
12. *Dermo-humeralis*, p. 13.	III. *Pars abdominalis*, p. 245.	(c) *Pectoralis abdominalis* (s. cutaneus) [inkl. Pect. abdom. meta-patagialis], p. 434.		

Description (for the crow and raven).

Pectoralis thoracica (Pect. tho.; figs. 4-6, 22).—This huge superficial muscle makes up the bulk of the breast meat. The origin is very extensive, including all of the postero-lateral portion of the sternum, all of the Cris. ster. ventral and posterior to the Sup. cor., almost the entire postero-lateral surface of the clavicle, and the anterior edge of the Mem. ster. cor. cl. (figs. 12-14). The fibers converge antero-laterally to the partly tendinous insertion on the ventral surface of the Cris. lat. hum. (fig. 12).

Pectoralis propatagialis longus (Pect. pro. l.; figs. 3, 5).—This short, tendinous slip arises from the antero-ventral surface of the belly of the Pect. tho. It passes laterally in the proximal portion of the prepatagial skin fold and becomes closely connected with the distal end of the belly of the Propat. l.

Pectoralis propatagialis brevis (Pect. pro. b.; fig. 6).—This is another tendinous slip

arising from the belly of the Pect. tho. It inserts on the proximal end of the tendon of the Propat. b.

Pectoralis abdominalis (Pect. abd.; figs. 2, 6).—This superficial, fleshy, ribbon-like dermal muscle arises from the skin along the side of the thorax and abdomen, beginning in the region of the knee, closely attached to the posterior end of the enlarged part of the ventral feather tract. It extends anteriorly close to the dorso-lateral border of the Pect. tho. and disappears in the axilla, between the dorsal surface of the Pect. tho. and the ventral surface of the Bic. bra. It usually inserts into the belly of the Pect. tho. and rarely into the posterior edge of the proximal tendon of the Bic. bra.

Action.—The Pect. tho. pulls the humerus forward and downward, furnishing most of the power for flight. The Pect. tho. assists the Propat. l. and b. in tensing the prepatagial

Fig. 6.—Crow, as in fig. 5, but with Cuc. propat., Propat. l., Pect. tho., Pect. pro. and Int. vol. wholly or partly removed. ×.6.

membrane. The Pect. abd. probably functions only to produce a slight ruffling of the feathers along the flank.

Innervation.—Branches of the *Nn. brachiales inferiores,* Gadow and Selenka, 1891, p. 211; Fürbringer, 1902, p. 342. *N. pectoralis,* Howell, 1937, p. 372. *N. brachialis longus inferior,* Fisher, 1946, p. 577.

Comparison.—Pect. tho.—Uniformly developed in all the specimens examined.

Pect. pro.—Similar in all forms.

Pect. abd.—Very uniformly developed in the various species studied. Insertion on the tendon of origin of the Bic. bra. was noted in only two specimens of *Corvus brachyrhynchos.* In all others the insertion was into the belly of the Pect. tho. We did not find any definite division of this muscle into anterior and posterior parts as described by Fürbringer (1902, p. 436).

M. SUPRACORACOIDEUS (Sup. cor.)

Pectoralis secundus, No. 50, Shufeldt, 1890, p. 72. *Supracoracoideus,* No. 74, Gadow and Selenka, 1891, p. 246. *Supracoracoideus,* No. 8, Fürbringer, 1902, p. 441. *Supracoracoideus,* Howell, 1937, p. 372. *Supracoracoideus,* Fisher, 1946, p. 578.

Description (for the crow and raven; figs. 3, 6, 8).—This deeply-situated muscle is the second most powerful associated with the shoulder joint and is exposed upon removal of the Pect. tho. It arises fleshy from a triangular area on the antero-lateral surface of the sternum, including the dorsal portion of the Cris. ster. not occupied by the Pect. tho., from about the ventro-basal half of the coracoid and most of the lateral surface of the Mem. ster. cor. cl. (figs. 12-14). The belly is bipinnate, the fibers converging upon a tendinous sheet which divides the muscle longitudinally. Anteriorly the belly narrows toward the shoulder joint and passes dorsally through the small space between the enlarged ends of the clavicle, coracoid and scapula. Upon reaching the dorsal side of the shoulder joint the muscle emerges as a strong tendon which turns abruptly laterad through an angle of about ninety degrees. It then passes over the dorsal surface of the humerus, between the Delt. maj. and Delt. min. to the insertion on the antero-dorsal edge of the *Caput humeri,* between the Tuber. lat. hum. and the Cris. lat. hum. (figs. 11, 16b). Just anterior to the humero-scapular bone the tendon passes through a strong fibro-cartilaginous pulley which holds it firmly in place. On the dorsal side of the shoulder the tendon of the Sup. cor. is partly visible superficially between the Delt. maj. and Delt. min.

Action.—Rotates the antero-dorsal edge of the humerus upward in the closed wing; elevates the humerus when the wing is extended.

Innervation.—A branch of the *Nn. brachiales inferiores.* Gadow and Selenka, 1891, p. 250; Fürbringer, 1902, p. 340. *N. supracoracoideus,* Howell, 1937, p. 372. *N. brachialis longus inferior* (?), Fisher, 1946, p. 579.

Comparison.—From the dorsal side, the tendon of insertion is concealed by the Delt. min. in *Aphelocoma, Cyanocorax, Cissolopha,* and *Calocitta.* In all others more or less of the tendon is visible posterior to the Delt. min.

M. CORACOBRACHIALIS ANTERIOR (Cor. bra. ant.)

Coraco-humeralis, No. 55, Shufeldt, 1890, p. 86. *Coraco-brachialis anterior,* No. 75, Gadow and Selenka, 1891, p. 251. *Coraco-brachialis externus s. anterior,* No. 9, Fürbringer, 1902, p. 452. *Coracobrachialis anterior,* Howell, 1937, p. 372. *Coracobrachialis anterior,* Fisher, 1946, p. 583.

Description (for the crow and raven; figs. 4, 6, 7, 9).—A small muscle on the anterior side of the shoulder joint adjacent to the antero-dorsal edge of the Pect. tho. It comes into view upon removal of the Propat. b., Delt. min. and Pect. tho. The Cor. bra. ant. arises from the dorsal end of the coracoid just anterior to the glenoid fossa and from the outer surface of the proximal end of the large coracohumeral ligament (figs. 12, 13). Insertion is on the anterior surface of the *Caput humeri,* just ventral to the insertion of the Sup. cor. (figs. 12, 16b). This rather ligamentous muscle appears to contain much fibrous connective tissue and its ability to contract is probably very limited.

Action.—Tends to draw the humerus anteriorly with perhaps a slight lifting motion.

Innervation.—Through the *Nn. brachiales inferiores,* Gadow and Selenka, 1891, p.

251; Fürbringer, 1902, p. 344. A branch of the *N. flexor brachii,* Howell, 1937, p. 368. *N. brachialis longus inferior,* Fisher, 1946, p. 583.

Comparison.—Similar in all forms examined.

M. CORACOBRACHIALIS POSTERIOR (Cor. bra. post.)

Pectoralis tertius, No. 51, Shufeldt, 1890, p. 74. *Coraco-brachialis posterior,* No. 76, Gadow and Selenka, 1891, p. 252. *Coraco-brachialis internus s. posterior,* No. 10, Fürbringer, 1902, p. 459. *Coracobrachialis posterior,* Howell, 1937, p. 372. *Coracobrachialis posterior,* Fisher, 1946, p. 579.

Description (for the crow and raven; figs. 4, 6, 8, 10).—Origin fleshy from a little less than the proximal half of the lateral surface of the coracoid and tendinous from a narrow curving line on the lateral side of the sternum adjacent to the ventro-medial edge of the origin of the Ster. cor. (figs. 12, 13). The fleshy belly extends antero-dorsally along
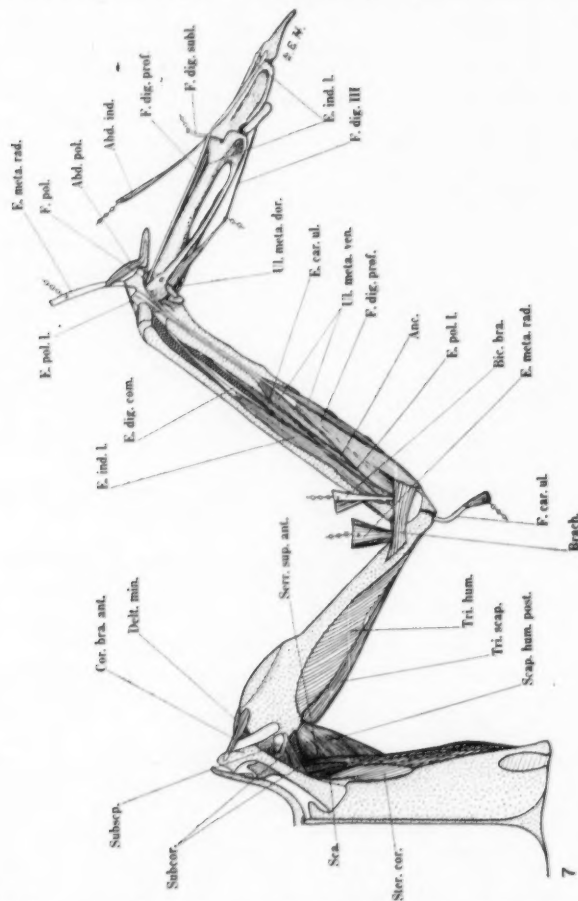
Fig. 7.—Crow, as in fig. 6, but with Abd. ind. displaced and Sup. cor., Cor. bra. post., Pect. abd., Bic. bra., E. meta. rad., pronators, F. car. ul., F. dig. subl. and Int. dor wholly or partly removed. ×.6.

the lateral side of the coracoid toward the posterior side of the shoulder joint. Insertion is by a short tendon which passes between the Subcor. and the Scap. hum. post. and attaches itself to the upper surface of the Tuber. med. hum. immediately behind the For. pneu. and adjacent to the proximal end of the ventral portion of the Tri. hum. (figs. 11, 16a). From the lateral side the Cor. bra. post. is exposed upon removal of the Pect. tho.

Action.—Helps to pull the humerus posteriorly, folding it against the body; possibly with a slight rotation.

Innervation.—Through the *Nn. brachiales inferiores*, Gadow and Selenka, 1891, p. 253; Fürbringer, 1902, p. 342. A branch from the root of the *N. pectoralis*, Howell, 1937, p. 368. Branches from the *N. brachialis longus inferior*, Fisher, 1946, p. 579.

Comparison.—In most specimens the origin of this muscle extends along about the posterior half of the coracoid. It was relatively shortest in *Corvus* and slightly longer in *Kitta* and *Cyanocorax*.

M. STERNOCORACOIDEUS (Ster. cor.)

Subclavius, No. 60, Shufeldt, 1890, p. 94. *Sterno-coracoideus*, No. 67, Gadow and Selenka, 1891, p. 224. *Sterno-coracoideus (superficialis et profundus)*, No. 6. Fürbringer, 1902, p. 410. *Sternocoracoideus*, Howell, 1937, p. 371. *Sternocoracoideus*, Fisher, 1946, p. 587.

Description (for the crow and raven; figs. 8-10).—This short, fleshy muscle arises from the entire ventral surface of the antero-lateral process of the sternum and to a slight extent from the adjacent lateral surfaces of the lower ends of several sternal ribs (figs. 12, 13). It inserts on a large triangular area on the dorsal surface of the proximal end of the coracoid, adjacent to the sterno-coracoidal articulation (fig. 14). On the lateral side this muscle is exposed by removal of the Pect. tho. and the Cor. bra. post. Inside the thorax it is visible upon removal of the viscera.

Action.—Tends to move the coracoid laterally and the anterior ribs forward and upward. The fleshy condition of this muscle suggests considerable freedom of movement in the sterno-coracoidal articulation.

Innervation.—A branch of the *Nn. thoracici inferiores*, Gadow and Selenka, 1891, p. 225; Fürbringer, 1902, p. 341. *N. sternocoracoideus*, Howell, 1937, p. 371.

Comparison.—No differences worth mentioning were noted in this muscle.

M. SUBCORACOIDEUS (Subcor.)

Coraco-brachialis, No. 61, and *Teres minor*, No. 62, Shufeldt, 1890, pp. 95, 96. *Subcoracoideus*, No. 72a, Gadow and Selenka, 1891, p. 238. *Caput coracoideum (M. subcoracoideus)*, No. 16a, of the *M. subcoracoscapularis*, Fürbringer, 1902, pp. 554, 558. *Subcoracoideus*, Howell, 1937, p. 370. *Subcoracoideus*, Fisher, 1946, p. 587.

Description (for the crow and raven; figs. 6-10).—This muscle consists of two small and widely separated heads which unite just before inserting. The ventral head arises mostly fleshy from a small area on the dorso-medial edge of the coracoid near the sternal end of that bone, and just antero-medial to the insertion of the Ster. cor. (fig. 14). The belly extends antero-dorsally toward the insertion.

The dorsal head is shorter and arises from a small area on the medial surface of the dorsal end of the coracoid and the adjacent scapula, in intimate contact with the anterior end of the P. int. M. subscp. (fig. 14). The belly extends postero-ventrally to meet the ventral head and both turn laterally before uniting. The combined muscle emerges in the axillary region between the coracoid and the Cor. bra. post. It inserts partly fleshy on the postero-ventral edge of the Tuber. med. hum., just dorso-proximal to the humeral head of the biceps (figs. 12, 16a).

The Subcor. is best viewed from the medial side after cutting away one-half of the pectoral girdle and removing the viscera. Laterally the distal end may be seen upon removal of the Pect. tho. and rotation of the humerus dorsally and anteriorly.

Gadow and Selenka (1891, p. 239) refer to a sternal connection of the Subcor., but we have found no such attachment in the Corvidae.

Action.—Tends to swing the humerus postero-ventrally against the trunk.

Innervation.—A branch of the *N. subcoracoscapularis* of the *Nn. brachiales superiores,* Gadow and Selenka, 1891, p. 211; Fürbringer, 1902, p. 334. *N. subcoracoideus* of the *Nn. axillares,* Howell, 1937, p. 366. A branch of the *N. brachialis longus superior,* Fisher, 1946, p. 587.

Comparison.—Similar in all forms. The inaccessible position of this muscle makes a detailed examination impossible without destruction of the specimen. However, from what could be seen in lateral view, the Subcor. is uniformly developed in all the species.

M. SUBSCAPULARIS (Subscp.)

Subscapularis, No. 65, Shufeldt, 1890, p. 101. *Subscapularis,* No. 72b, Gadow and Selenka, 1891, p. 240. Subscapular heads, Nos. 16b and c, of the *M. subcoracoscapularis,* Fürbringer, 1902, pp. 554, 555, 559, 560. *Subscapularis,* Howell, 1937, p. 370. *Subscapularis,* Fisher, 1946, p. 584.

Description (for the crow and raven; figs. 4, 7-10).—The P. ext. and P. int. are intimately fused at their origin and insertion but are clearly separable throughout most of their extent, being separated by the flat tendon of insertion of the Serr. sup. ant. The
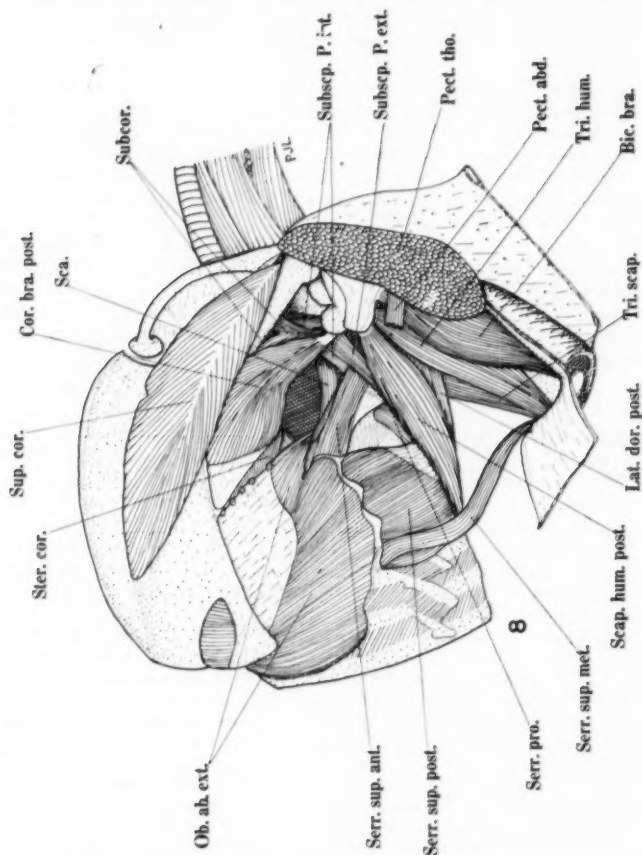
Fig. 8.—Crow. Lateral view of left axillary region with Pect. tho. and Pect. abd. mostly removed. ×.8.

origin of the P. ext. is fleshy from the lateral side of a little less than the proximal half of the shaft of the scapula (figs. 11, 13). The P. int. arises fleshy from the ventro-medial surface of about the proximal two-thirds of the scapula (fig. 14). The P. int. is much stronger than the P. ext. The two heads unite distally to form a short but powerful tendon which inserts on the proximal edge of the Tuber. med. hum., just dorsal and proximal to the insertion of the Subcor. (figs. 12, 16a).

Action.—Tends to swing the humerus posteriorly against the trunk and rotate the posterior edge of the wing upward.

Innervation.—Branches of the *N. subcoracoscapularis* of the *Nn. brachiales superiores*, Gadow and Selenka, 1891, p. 211; Fürbringer, 1902, p. 334. *N. subscapularis* of the *Nn. axillares*, Howell, 1937, p. 366. From the *N. brachialis longus superior*, Fisher, 1946, p. 584.

Comparison.—In many specimens the Subscp. extends along about the anterior half of the post-glenoid scapula; in *Corvus* more than half, and in *Perisoreus, Pica, Psilorhinus, Kitta, Cissolopha, Calocitta,* and *Cyanolyca* somewhat less than half.

M. CUCULLARIS, PARS PROPATAGIALIS (Cuc. propat.)

Dermo-tensor patagii, No. 6, Shufeldt, 1890, pp. 4, 7. *Pars Propatagialis M. Cucullaris,* No. 77:IV, Gadow and Selenka, 1891, p. 255. *Cucullaris propatagialis,* No. 1e, Fürbringer, 1902, p. 362. *Dermo-tensor patagii,* Fisher, 1946, p. 574.

Description (for the crow and raven; figs. 1, 5, 22, 23).—This small fleshy slip from the cucullaris detaches itself from the main portion of that muscle near the upper end of the clavicle and extends laterally in the prepatagial skin fold in close association with the Propat. l. It appears to insert partly by a short tendon on the distal end of he belly of the Propat. l., but mainly on the follicles of the anterior feathers of the humeral tract.

Action.—Ruffles some feathers of the lateral cervical region and anterior scapulars. Assists other patagial muscles in tensing the prepatagium.

Innervation.—According to Fürbringer (1902, p. 370) the cucullaris is supplied by a branch of the *N. vago-accessorius* and cervical nerves.

Comparison.—Very similar in all specimens examined.

M. PROPATAGIALIS LONGUS (Propat. l.)

Tensor patagii longus, No. 67, Shufeldt, 1890, p. 114. *Propatagialis longus,* No. 77:A, Gadow and Selenka, 1891, p. 255. *Propatagialis longus,* Fürbringer, 1902, p. 515. *Tensor patagii longus,* Fisher, 1946, p. 573.

Description (for the crow and raven; figs. 1, 5, 6, 22-29).—A small muscle arising from the anterior end of the terminal expansion of the clavicle in common with the Propat. b. (figs. 11-13). The belly extends laterally in the prepatagial skin fold and terminates about opposite the end of the proximal third of the humerus in a strong fibro-elastic tendon which continues distally to the wrist joint. Shortly before reaching the end of the radius it branches into two diffuse and rather poorly-defined but partly shiny inelastic tendons. These spread out and insert over much of the anterior side of the wrist. The anterior branch inserts partly on the proximal end of the pollex, on both the dorsal and ventral sides (figs. 11, 20e). The posterior portion inserts mainly on the antero-distal edge of the radius and on the *Os radiale.*

Action.—Tenses the anterior edge of the prepatagium; probably helps to extend the pollex.

Innervation.—From the *Nn. brachiales superiores*, Gadow and Selenka, 1891. p. 211. *N. axillaris,* Fürbringer, 1902, p. 336. A branch of the *N. brachialis longus superior,* Fisher, 1946, p. 573.

Comparison.—Similar in all forms examined, but belly shorter in *Calocitta* and *Cyanolyca.*

M. PROPATAGIALIS BREVIS (Propat. b.)

Tensor patagii brevis, No. 68, Shufeldt, 1890, p. 115. *Propatagialis brevis,* No. 77:B, Gadow and Selenka, 1891, p. 256. *Propatagialis brevis,* Fürbringer, 1902, p. 517. *Tensor patagii brevis,* Fisher, 1946, p. 576.

Description (for the crow and raven; figs. 1, 2, 6, 22-25).—This muscle is several times the size of the Propat. l., with which it arises in common from the anterior end of the dorsal expansion of the clavicle (figs. 11-13). A little beyond the distal end of the Cris. lat. hum. the belly receives the inelastic tendon of the Pect. pro. b. and terminates in a strong inelastic tendon which passes distally, enclosed in the posterior portion of the prepatagium. The tendon is strongly inserted into the anterior side of the proximal portion of the belly of the E. meta. rad. From the point of attachment on this muscle the tendon of the Propat. b. extends to its final insertion on the lateral epicondyle of the humerus, between the terminal insertion of the Delt. maj. and the origin of the E. dig. com. (figs. 11, 16a).

Action.—Assists the Bic. bra. in flexing the forearm; also helps the Propat. l. in tensing the prepatagium.

Innervation.—From the *Nn. brachiales superiores*, Gadow and Selenka, 1891, p. 211. *N. axillaris*, Fürbringer, 1902, p. 336. A branch of the *N. brachialis longus superior*, Fisher, 1946, p. 576.

Comparison.—Very uniformly developed.
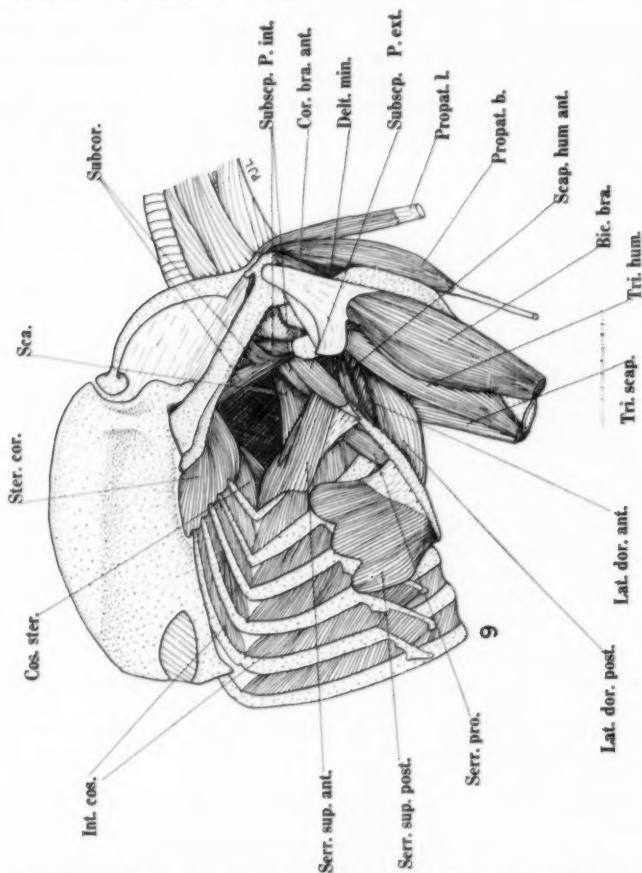
Fig. 9.—Crow, as in fig. 8, but with Pect., Sup. cor., Cor. bra. post., Scap. hum. post., Serr. sup. met. and Ob. ab. ext. removed. ×.8.

M. DELTOIDEUS MAJOR (Delt. maj.)

Deltoid, No. 70, Shufeldt, 1890, p. 117. *Deltoideus major*, No. 69, Gadow and Selenka, 1891, p. 230. *Deltoides major*, No. 14b, Fürbringer, 1902, p. 525. *Deltoidus*, Burt, 1930, p. 491; Howell, 1937, p. 370. *Deltoideus major*, Fisher, 1946, p. 589.

Description (for the crow and raven; figs. 1, 2, 22-24).—Superficial throughout and divided into two parts which fuse distally.

Deltoideus major anterior (Delt. maj. ant.).—This fleshy belly is several times the bulk of the posterior head. It arises fleshy from a small area on the dorsal side of the scapula opposite the glenoid fossa, from the Os hum. scap. and adjacent ligaments. Insertion is on most of the upper surface of the large Cris. lat. hum. and partly tendinous on a long narrow line down the antero-dorsal margin of about the proximal three-fourths of the Corp. hum. (figs. 11, 16a and b). At the distal end the muscle converges into a very narrow tendon which inserts on the proximal end of the Epicon. lat. hum. (figs. 11, 16a).

Deltoideus major posterior (Delt. maj. post.).—This fleshy part arises from an extensive area on the dorsal end of the clavicle and a small area on the adjacent scapula (figs. 11, 14). It inserts on the posterior side of the Delt. maj. ant. about midway the brachium. A strong tendinous band extends from the scapula and is attached to the posterior margin of the muscle near the proximal end.

Action.—Elevates the humerus and swings it posteriorly against the trunk.

Innervation.—A branch of the *N. radialis* of the *Nn. brachiales superiores*, Gadow and Selenka, 1891, p. 233. *N. axillaris* of the *Nn. brachiales superiores*, Fürbringer, 1902, p. 360. One of the *Nn. axillares*, Howell, 1937, p. 366. A branch of the *N. brachialis longus superior*, Fisher, 1946, p. 590.

Comparison.—There is some slight variation in the length of the distal tendon of insertion, this being relatively slightly longer in *Corvus, Cyanocitta, Pica, Gymnorhinus, Nucifraga, Cyanocorax* and *Psilorhinus*, and somewhat shorter in the other forms examined.

Generally in the smaller species of Corvidae the Delt. maj. is relatively broader in comparison to its length than in the larger forms such as *Corvus* and *Nucifraga*.

Approximate breadth-length ratio

Cyanolyca	37	*Garrulus*	29
Aphelocoma coerulescens californica	36	*Cyanocorax*	29
A. c. insularis	35	*Pica*	28
A. ultramarina	35	*Psilorhinus*	28
Cyanocitta	34	*Kitta*	26
Calocitta	34	*Cissolopha yucatanica*	25
Cissolopha beecheyi	33	*Nucifraga*	24
Perisoreus	31	*Corvus brachyrhynchos*	24
Aphelocoma c. coerulescens	30	*C. corax*	23
Gymnorhinus	30		

M. DELTOIDEUS MINOR (Delt. min.)

Scapulo-humeralis, No. 56, Shufeldt, 1890, p. 86. *Deltoideus minor*, No. 70, Gadow and Selenka, 1891, p. 234. *Deltoides minor*, No. 14c, Fürbringer, 1902, p. 535. *Deltoideus*, deep brevis, Howell, 1937, p. 370. *Deltoideus minor*, Fisher, 1946, p. 583.

Description (for the crow and raven; figs. 2, 3, 7).—A very small, entirely fleshy, ribbon-like muscle located on the dorsal side of the shoulder joint. The proximal end is covered by the Delt. maj. post. and the distal end by the Propat. b.

The origin is from a small area on the dorso-anterior apex of the scapula, lateral and adjacent to the scapular origin of the Delt. maj. post. (fig. 11). The belly passes over the joint capsule and inserts on the dorsal side of the *Caput humeri* just proximal to the upper end of the insertion of the Delt. maj. ant. and distal to the insertion of the Supcor. (figs. 11, 16b).

Action.—Tends to move the humerus anteriorly and dorsally.

Innervation.—*N. radialis*, Gadow and Selenka, 1891, p. 235. *N. axillaris*, Fürbringer,

1902, p. 540. One of the *Nn. axillares*, Howell, 1937, p. 366. A branch of the *N. brachialis longus superior*, Fisher, 1946, p. 583.

Comparison.—Very uniformly developed.

M. TRICEPS BRACHII (Tri. bra.)

Triceps, No. 71, Shufeldt, 1890, p. 119. *Triceps cubiti s. anconaeus*, No. 81, Gadow and Selenka, 1891, p. 263. *Anconaeus*, No. 17, Fürbringer, 1902, p. 563. *Triceps brachii*, Burt, 1930, p. 491. *Triceps*, Howell, 1937, p. 371. *Triceps*, Fisher, 1946, p. 590.

Description (for the crow and raven; figs. 1-7, 22-24).—The triceps consists of two distinct parts, a Tri. scap. from the scapula and a Tri. hum. from the posterior surface of the humerus. The latter is divided proximally for a short distance into a dorsal head and a ventral head.

Triceps scapularis (Tri. scap.).—Origin mainly fleshy from the dorsal surface of the scapula just medial to the posterior border of the glenoid fossa and from the adjacent joint capsule (figs. 11, 13). The long slender belly makes up the posterior border of the brachial musculature. Shortly above the elbow it converges to form a flat tendon which fuses with the dorsal portion of the Tri. hum. and encloses a small sesamoid (fig. 4). Insertion is on the dorso-proximal surface of the ulna, between the base of the olecranon and the coronoid process (figs. 11, 17b).

Triceps humeralis (Tri. hum.).—Origin fleshy from most of the posterior surface of the humerus, from the For. pneu., to a point just above the distal condyles (figs. 11, 12, 16a). Proximally it is divided by the insertion of the Scap. hum. ant. into the dorsal and ventral heads which are separable for about the proximal one-third of the muscle. The dorsal head is interrupted slightly on its dorsal edge by the insertion of the Lat. dor. post. The proximal end of the ventral head is notched slightly by the insertion of the Scap. hum. post. The Tri. hum. is more than twice the bulk of the Tri. scap. Insertion is fleshy on the dorso-anterior side of the olecranon and tendinous on the apex of that process (figs. 11, 12, 17b and d). Just above the elbow joint the ventral edge of the Tri. hum. forms a strong tendon (fig. 4).
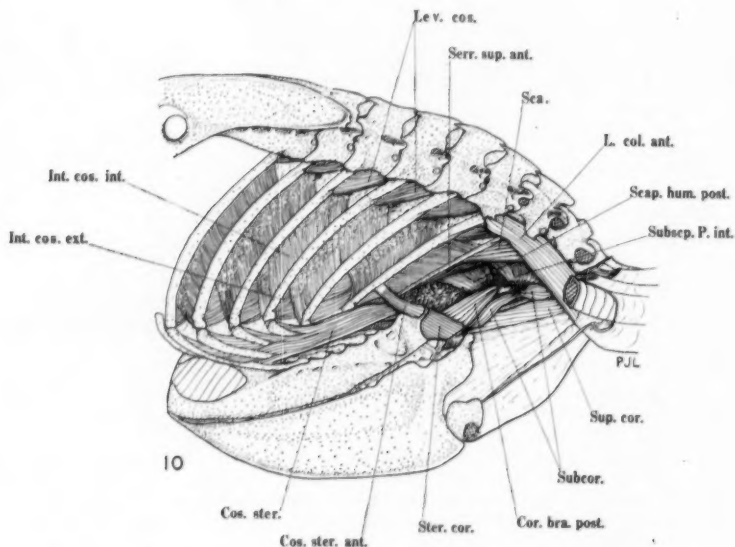
Fig. 10. Crow. Medial view of left half of thorax. Viscera and right side of sternum, clavicle and ribs removed. ×8.

The triceps muscle is mainly superficial but proximally it is partly concealed on the dorsal side by the Delt. maj. post., and on the ventral side by the Pect. tho. and the Bic. bra.

Action.—Extends forearm; the Tri. scap. also tends to draw the upper arm posteriorly against the trunk.

Innervation.—Branches of the *N. musculo-spiralis*, Gadow and Selenka, 1891, p. 265. *N. radialis*, Fürbringer, 1902, p. 570; Howell, 1937, p. 371. Branches of the *N. brachialis longus superior*, Fisher, 1946, p. 590.

Comparison.—Very uniformly developed in all species. The small sesamoid located in the tendon of insertion of the scapular head was present in all specimens examined with the exception of nearly grown nestlings of crows and ravens.

M. BICEPS BRACHII (Bic. bra.)

Biceps, No. 69, Shufeldt, 1890, p. 116. *Biceps brachii*, No. 79, Gadow and Selenka, 1891, p. 261. *Biceps brachii*, No. 11a, Fürbringer, 1902, p. 466; Burt, 1930, p. 490. *Biceps*, Howell, 1937, p. 375. *Biceps*, Fisher, 1946, p. 588.

Description (for the crow and raven; figs. 1-7, 22-25).—Origin by two tendons which unite opposite the *Caput humeri*. The longer head arises from the antero-lateral surface of the upper end of the coracoid (figs. 12, 13), the shorter from the Cris. med. hum. (figs. 12, 16a). The belly is superficial after emerging from beneath the Pect. tho. and extends along the ventro-anterior side of the Corp. hum. Beyond the elbow joint the short tendon of insertion disappears between the Pron. subl. and the E. meta. rad. At the distal end the tendon bifurcates into short branches. The smaller of these inserts on the Tuber. rad. (figs. 12, 17a), the larger on the ventro-proximal surface of the ulna, adjacent to the extreme proximal end of the anterior head of the F. dig. prof. (figs. 12, 17d).

Action.—Flexes forearm against upper arm in opposition to the triceps.

Innervation.—A branch of the *Nn. brachiales inferiores*, Gadow and Selenka, 1891, p. 262; Fürbringer, 1902, p. 359. *N. flexor brachii*, Howell, 1937, p. 368. A branch of the *N. brachialis longus inferior*, Fisher, 1946, p. 589.

Comparison.—Similar in all corvids studied.

In some birds the belly of the biceps gives rise to a mostly fleshy slip that extends anteriorly into the prepatagium and inserts on the tendon of the Propat. 1. (fig. 34). According to Gadow and Selenka (1891, p. 255) the biceps propatagialis (Bic. pro.) is present in cranes, gulls, auks, pigeons and many others. It is absent in the Corvidae.

M. EXPANSOR SECUNDARIORUM (Exp. sec.)

Expansor secundariorum, Shufeldt, 1890, p. 78. *Expansor secundariorum*, No. 78:III, Gadow and Selenka, 1891, p. 259. *Expansor secundariorum*, Fürbringer, 1902, p. 575.

Description (for the crow and raven; figs. 5, 25, 26).—This small triangular muscle is visible superficially on the posterior side of the forearm just distal to the olecranon. It arises tendinous from the posterior surface of the heavy ligament which passes between the ventral end of the Epicon. med. hum. and the base of the olecranon. The tendon of origin of the F. car. ul. is held in place on the posterior side of the elbow joint by the ligament just mentioned and the belly of the Exp. sec. which passes over the outer surface of this tendon. From the point of origin the muscle broadens out in a dorso-distal direction into a flat sheet which inserts mostly fleshy on the ventral side of the calamus of each of the three proximal secondary remiges and one adjacent tertiary. The Exp. sec. is often paler in color and tougher than surrounding muscles and probably has limited power of contraction due to the fibrous connective tissue permeating its belly.

Action.—Tends to draw the proximal secondary remiges ventro-medially.

Innervation.—*N. cutaneus brachii superior* of the *Nn. brachiales superiores*, Fürbringer, 1902, p. 338.

Comparison.—Similar in all corvids studied.

In many birds, for example falcons and grouse, this muscle has a fan-shaped belly inserting on the proximal secondaries about as in the crow but in addition has a muscular slip extending proximally in the posterior border of the metapatagial skin fold (figs. 33,

Fig. 11.—Crow. Dorsal view of wing skeleton showing muscle attachments. ×.6.

35); about one-third the way up the humerus from the elbow this slip changes into a long, slender tendon which extends proximally into the axillary region.

M. BRACHIALIS (Brach.)

Brachialis anticus, No. 72, Shufeldt, 1890, p. 121. *Brachialis inferior,* No. 80, Gadow and Selenka, 1891, p. 262. *Brachialis inferior,* No. 12, Fürbringer, 1902, p. 478. *Brachialis,* Howell, 1937, p. 375. *Brachialis,* Fisher, 1946, p. 591.

Description (for the crow and raven; figs. 5-7, 25).—A short, entirely fleshy, band-like muscle arising from a narrow area on the anterior side of the ventral ridge of the humerus, just proximal to the Epicon. med. hum. (figs. 12, 16b). The belly passes diagonally distad across the elbow joint, ventral to the tendon of the Bic. bra., to the insertion on the ventro-posterior surface of the proximal end of the ulna, between the two heads of the F. dig. prof. (figs. 12, 17b).

Action.—Assists the biceps in flexing the forearm against the brachium.

Innervation.—A branch of the *N. brachialis longus inferior,* Gadow and Selenka, 1891, p. 263; Fürbringer, 1902, p. 480; Fisher, 1946, p. 591. *N. flexor brachii,* Howell, 1937, p. 368.

Comparison.—No variations noted.

M. PRONATOR SUBLIMIS (Pron. subl.)

Pronator brevis, No. 77, Shufeldt, 1890, p. 129. *Pronator sublimis* of *Mm. entepicondylo-radiales,* No. 82 A-I, Gadow and Selenka, 1891, p. 267. *Pronator brevis,* Fisher, 1946, p. 594.

Description (for the crow and raven; figs. 4, 5, 25-27).—A superficial muscle of the ventral surface of the forearm, arising by a short, flat tendon from the proximal end of the Epicon. med. hum., just distal to the origin of the Brach. (figs. 12, 16a and b). The belly extends distally between the E. meta. rad. and the Pron. prof. to the partly fleshy insertion on a narrow line along the ventral side of the Corp. rad. about midway the forearm (figs. 12, 17a).

Action.—Tends to move the distal end of the forearm and wrist ventrally. Since the origin is located so close to the distal end of the humerus it is doubtful that this muscle has any influence in flexing the forearm.

Innervation.—Branches of the *N. medianus,* Gadow and Selenka, 1891, p. 268. Branches of the *N. brachialis longus inferior,* Fisher, 1946, p. 594.

Comparison.—In *Corvus* the pronator muscles are confined to about the proximal half of the forearm. In all others examined they extend farther distally, often as much as two-thirds the length of the forearm.

M. PRONATOR PROFUNDUS (Pron. prof.)

Pronator longus, No. 78, Shufeldt, 1890, p. 132. *Pronator profundus* of *Mm. entepicondylo-radiales,* No. 82A-II, Gadow and Selenka, 1891, p. 267. *Pronator longus,* Fisher, 1946, p. 594.

Description (for the crow and raven; figs. 5, 6, 25-27).—Most of the Pron. prof. is concealed ventrally by the Pron. subl. and at the proximal end to a slight extent by the F. dig. subl. It is somewhat greater in bulk than the Pron. subl. The origin is mainly tendinous from the Epicon. med. hum. (figs. 12, 16b), between the origins of the Pron. subl. and the F. dig. subl. The tendon of origin is also attached along its posterior edge to the adjacent humero-ulnar pulley. The thick belly flattens out distally, forming a thin sheet which inserts partly fleshy on a very long, narrow line along the ventral surface of radius, partly proximal to the insertion of the Pron. subl. (figs. 12, 17a). The length of this attachment to the radius is considerably longer than that of the Pron. subl.

Action.—Assists the Pron. subl. in depressing the distal end of the forearm.

Innervation.—Branches from the *N. medianus,* Gadow and Selenka, 1891, p. 268. Branches from the *N. brachialis longus inferior,* Fisher, 1946, p. 594.

Comparison.—In the majority of cases the Pron. prof. ends at about the same point as the distal end of the Pron. subl. In *Cyanocorax* and *Kitta* the Pron. prof. does not extend as far distally as the Pron. subl.
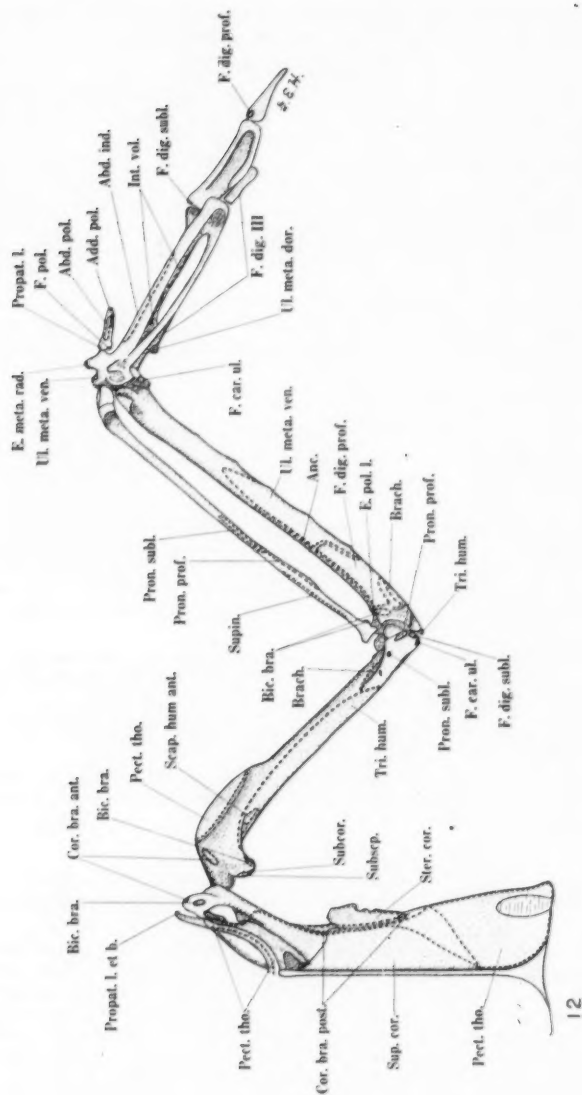
Fig. 12.—Crow. Ventral view of pectoral girdle and wing skeleton showing muscle attachments. Scapula removed ×.6.

M. ENTEPICONDYLO-ULNARIS (Ent. ul.)

Entepicondylo-ulnaris, No. 82B, Gadow and Selenka, 1891, p. 267.

This muscle is absent in most birds, including the Corvidae. According to Gadow and Selenka (1891, p. 267) it is found only in the "Rasores," including the tinamous. In the blue grouse (*Dendragapus obscurus*) it arises from the Epicon. med. hum. in common with the Pron. prof. and inserts fleshy on the ventral surface of the ulna, proximal to the F. dig. prof. and the Ul. meta. ven. (fig. 35). Superficially it is concealed by the F. car. ul.

Action.—Assists the pronators in depressing the distal end of the forearm.

Innervation.—Through the *N. medianus*, Gadow and Selenka, 1891, p. 268.

M. FLEXOR CARPI ULNARIS (F. car. ul.)

Flexor carpi ulnaris, No. 83, Shufeldt, 1890, p. 141. *Flexor carpi ulnaris s. entepicondylo-carpalis*, No. 85, Gadow and Selenka, 1891, p. 270. *Flexor carpi ulnaris*, Fisher, 1946, p. 598.

Description (for the crow and raven; figs. 3-6, 25-29).—The F. car. ul. makes up the posterior border of the musculature of the forearm. It arises by a strong tendon from the surface of the Epicon. med. hum. just postero-dorsal to the origin of the F. dig. subl. (figs. 12, 16a). The tendon of origin passes through the humero-ulnar pulley immediately ventral to the olecranon. The Exp. sec. lies upon this tendon of origin. The belly, extending about three-fifths the length of the forearm, divides distally, the heavier portion continuing tendinous within a heavy sheath with the F. dig. subl., the smaller division continuing as a fine tendon running dorso-posterior to the ensheathed mass. Both tendons insert upon the ulnare, the fine tendon dorsally to the heavier (figs. 12, 18c).

Fibrous connections between the sheath and free tendon are attached to the bases of the four distal secondaries; the dorsal surface of the belly of the F. car. ul. supplies fibrous attachments to the two more proximal secondaries.

The posterior muscle mass of the forearm, composed of the F. car. ul. and F. dig. subl., is partly enclosed within a tendinous sheath, having a tough fibrous band extending along the postero-ventral surface from the Epicon. med. hum. to the proximal and ventral sides of the *Os ulnare* (figs. 5, 28). The distal portion of this tendinous sheath spreads out in various directions over the ventral side of the wrist joint.

Action.—This is the principal muscle flexing the hand against the forearm. It is also important in folding the secondary remiges against the posterior side of the forearm. Because of the attachment to the humerus there is probably a tendency to extend the forearm.

Innervation.—A branch of the *N. ulnaris*, Gadow and Selenka, 1891, p. 271. Branches of the *N. brachialis longus inferior*, Fisher, 1946, p. 598.

Comparison.—Similar in all forms.

M. FLEXOR DIGITORUM SUBLIMIS (F. dig. subl.)

Described as a part of the *Flexor carpi ulnaris*, No. 83, Shufeldt, 1890, p. 141; Fisher, 1946, p. 598. *Flexor digitorum sublimis*, No. 90, Gadow and Selenka, 1891, p. 278. *Flexor metacarpi ulnaris*, Burt, 1930, p. 496.

Description (for the crow and raven; figs. 4-7, 25-31).—Distally the F. dig. subl. is ensheathed with the F. car. ul. It arises fleshy from about the proximal one-fourth of the internal face of the heavy tendinous band originating upon the Epicon. med. hum. between the origin of the Pron. prof. and the F. car. ul. (figs. 12, 16b). The fusiform belly extends along the proximal one-third to two-fifths of the ulna. The tendon passes within the sheath to the wrist joint where it winds around the anterior face of the *Os ulnare* and extends diagonally across the ventral surface of Meta. II; in company with the tendon of the F. dig. prof. it continues to the base of the index digit. At this point the tendon of the F. dig. subl. inserts on the antero-proximal edge of Phal. I, Dig. II (figs. 11, 12, 19, 20c).

Action.—Assists the F. car. ul. in flexing the hand against the forearm. Because of its insertion on the anterior side of the wing the F. dig. subl. also tends to depress the hand and extend the index digit.

Innervation.—A branch of the *N. medio-ulnaris*, Gadow and Selenka, 1891, p. 279.

Branches from the posterior trunk of the *N. brachialis longus inferior*, Fisher, 1946, p. 598.

Comparison.—The muscle itself is similar in all forms studied, but there is a difference in the relationship of the belly to the tendinous band with which it is associated. In *Corvus* and *Nucifraga* the belly is almost entirely concealed ventrally by the heavy tendi-
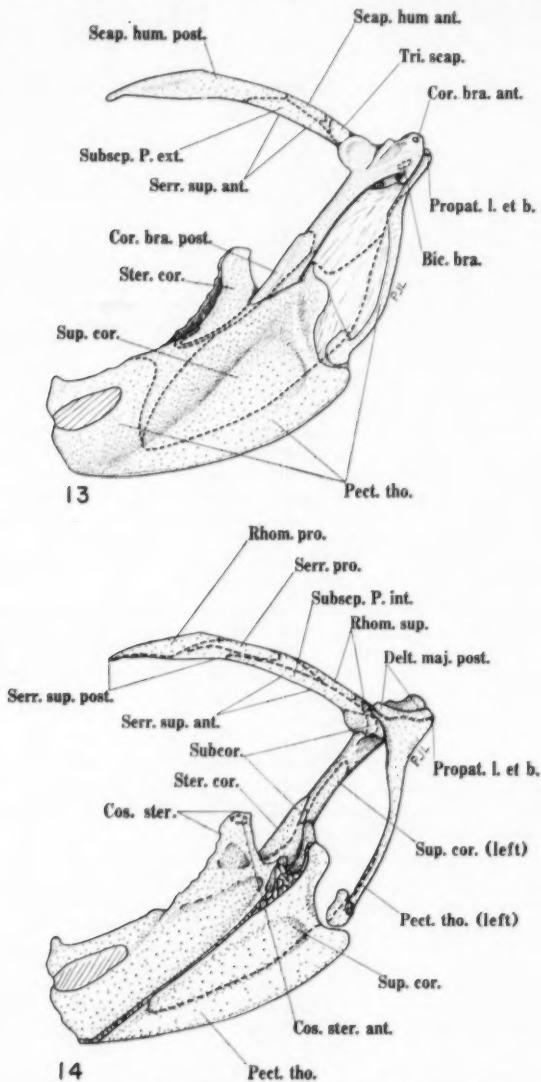
Figs. 13, 14. Crow.—13. Lateral view of pectoral girdle showing muscle attachments. ×.8; 14. Medial view of pectoral girdle showing muscle attachments. Right half of girdle removed. ×.8.

nous band. In all others examined the belly is superficial ventrally and the tendinous band greatly reduced.

M. FLEXOR DIGITORUM PROFUNDUS (F. dig. prof.)

Flexor digitorum profundus, No. 82, Shufeldt, 1890, p. 139. *Flexor digitorum profundus*, No. 91, Gadow and Selenka, 1891, p. 279. *Flexor digitorum profundus*, Fisher, 1946, p. 597.

Description (for the crow and raven; figs. 3-7, 26-32).—The F. dig. prof. is exposed by the removal of both pronator muscles, the F. dig. subl. and F. car. ul. At the proximal end the F. dig. prof. is divided into two short bellies by the insertion of the brachialis (fig. 7). One head arises from the posterior border of the ulna, distal to the olecranon, and crosses the brachialis to be joined by a second head originating from the ventral surface of the ulna. The fleshy origin is from about the proximal two-fifths of the ventral surface of the ulna (figs. 12, 17b and d). The belly extends slightly beyond the middle of the forearm and passes distally along the postero-ventral side of the Ul. meta. ven. At the wrist joint the tendon is held firmly in place by stout ligaments and wraps around the anterior side of the Tuber. musc. of the carpometacarpus. Beyond the base of the pollex the tendon passes along the antero-ventral surface of Meta. II to the base of the index digit in close association with the tendon of the F. dig. subl. From this point it passes distally, bound closely to the antero-ventral ridge of the proximal phalanx, to its insertion on the ventral side of the proximal end of the distal phalanx (figs. 12, 20d).

Action.—Assists the F. car. ul. in flexing the hand against the forearm when the wing is in the extended position. As the wing is folded more closely this flexor action is lost and any further contraction tends to depress the hand. There is also a tendency to extend the index digit.

Innervation.—A branch of the *N. medianus*, Gadow and Selenka, 1891, p. 281. The anterior branch of the *N. brachialis longus inferior*, Fisher, 1946, p. 597.

Comparison.—In *Corvus* the belly of the F. dig. prof. ends decidedly proximal to the end of the belly of the Ul. meta. ven. The two bellies end at about the same point in *Aphelocoma, Gymnorhinus, Cyanocorax, Kitta, Calocitta*, and *Cyanolyca*. All other specimens were intermediate.

M. ULNIMETACARPALIS VENTRALIS (Ul. meta. ven.)

Flexor carpi ulnaris brevior, No. 84, Shufeldt, 1890, p. 144. *Ulni-metacarpalis ventralis*, No. 86, Gadow and Selenka, 1891, p. 272. *Flexor carpi ulnaris brevis*, Fisher, 1947, p. 598.

Description (for the crow and raven; figs. 5-7, 27-29).—Origin fleshy from the ventral and posterior surfaces of the ulna, extending from the areas of origin of the F. dig. prof. and the anconeus to the proximal end of about the distal third of the ulna (figs. 12, 17b and d). The slender tendon runs distally in close association with the anterior side of the tendon of the F. dig. prof. On the ventral side of the wrist joint the tendon is held firmly in place by ligaments and fascia. Distally it broadens out and disappears beneath the Abd. pol. and the tendon of the E. meta. rad. and extends dorsad to its insertion on the antero-ventral surface of the proximal end of the carpometacarpus, adjacent to the proximal side of Meta. I (figs. 12, 20b).

From the ventral side most of the Ul. meta. ven. is exposed by removal of the F. dig. prof.

Action.—Functions mainly as a pronator of the hand. In the extended wing it also tends to flex the hand against the forearm.

Innervation.—Through the *N. medio-ulnaris*, Gadow and Selenka, 1891, p. 273. A branch of the anterior branch of the *N. brachialis longus inferior*, Fisher, 1946, p. 599.

Comparison.—No differences noted.

M. EXTENSOR METACARPI RADIALIS (E. meta. rad.)

Extensor metacarpi radialis longior, No. 73, Shufeldt, 1890, p. 124. *Extensor metacarpi ulnaris.* This is a typographical error and should be *Extensor metacarpi radialis*, No. 88, Gadow and Selenka, 1891, p. 274. *Extensor metacarpi radialis longus*, Burt, 1930, p. 492. *Extensor metacarpi radialis*, Fisher, 1946, p. 591.

Description (for the crow and raven; figs. 1-3, 5-7, 25-29).—This is the most powerful muscle of the forearm. It arises tendinous from the apex of the Epicon. lat. hum. and mostly fleshy from a large area on the anterior surface of the distal end of the humerus just proximal to the capitulum (figs. 11, 16a and b). These two areas of origin are separated slightly by the passage of the *N. radialis*. The belly extends along the anterior side of about the proximal three-fifths of the radius and beyond this the strong tendon continues
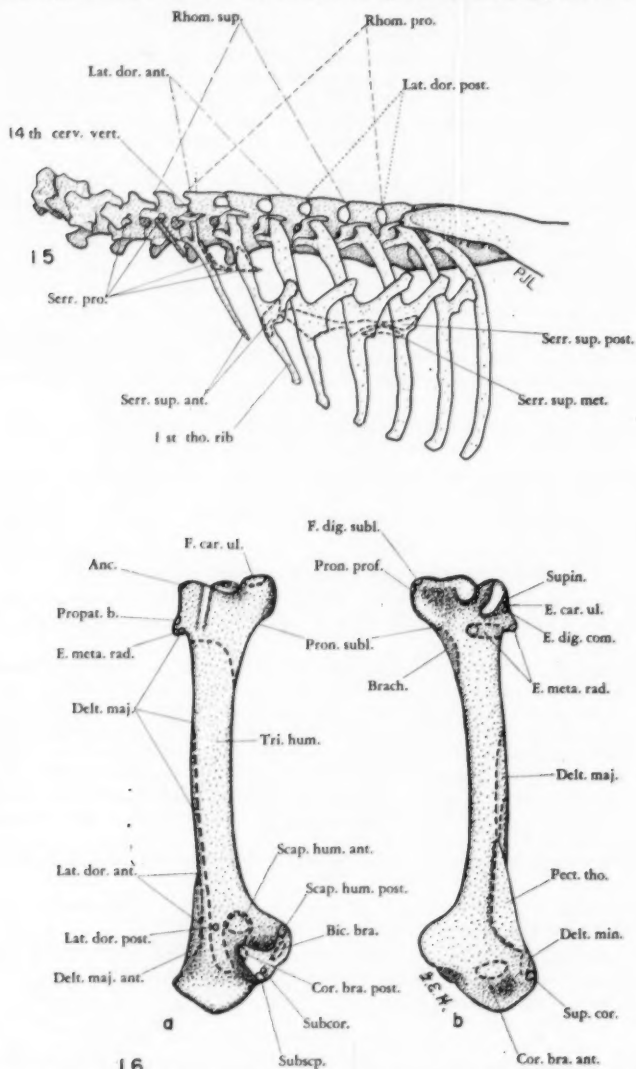
Figs. 15, 16. Crow.—15. Lateral view of vertebral ribs and adjacent vertebrae, showing muscle attachments. ×.8; 16. Humerus, showing muscle attachments. ×.9.—a. Posterior surface; b. anterior surface.

toward the insertion on the antero-proximal side of Meta. I (figs. 11, 12, 20b). At the wrist the tendon glides through a broad groove on the antero-dorsal side of the distal end of the radius and on the *Os radiale*. Near the proximal end of the belly this muscle is strongly attached to the tendon of insertion of the Propat. b.

Action.—Powerful extension of the hand. There may also be a tendency to flex the forearm against the brachium.

Innervation.—A branch of the *N. radialis*, Gadow and Selenka, 1891, p. 276. Branches of the *N. brachialis longus superior*, Fisher, 1946, p. 592.

Comparison.—Compared to the other forms studied the belly appears relatively stouter in *Perisoreus*, *Cyanocitta*, *Aphelocoma*, *Calocitta*, and *Cyanolyca*. In most specimens the belly extends along about the proximal two-thirds of the forearm; it is slightly shorter in *Perisoreus*, *Pica*, and *Corvus*.

M. SUPINATOR (Supin.)

Supinator brevis. No. 75, Shufeldt, 1890, p. 127. *Ectepicondylo-radialis*, No. 84, Gadow and Selenka, 1891, p. 269. *Supinator brevis*, Fisher, 1946, p. 593.

Description (for the crow and raven; figs. 2, 3, 25, 26).—An extremely small muscle located along the antero-proximal border of the radius and partly covered dorsally by the E. meta. rad. and the E. dig. com. It arises by a short tendon from the Epicon. lat. hum., close to the points of origin of the E. car. ul. and the anconaeus (fig. 11). Insertion is fleshy on the anterior border of about the proximal third of the Corp. rad. (figs. 11, 17c).

Action.—Tends to elevate the anterior border of the forearm. There is probably a slight tendency to flex the forearm against the brachium.

Innervation.—A branch of the *N. radialis*, Gadow and Selenka, 1891, p. 270. A branch of the anterior trunk of the *N. brachialis longus superior*, Fisher, 1946, p. 593.

Comparison.—This muscle is confined to about the proximal one-third of the forearm in most forms. It extends a little farther distally in most specimens of *Aphelocoma* and in *Psilorhinus*. The belly appears somewhat stouter in *Cyanocorax*.

M. EXTENSOR DIGITORUM COMMUNIS (E. dig. com.)

Extensor digitorum communis, No. 74, Shufeldt, 1890, p. 125. *Extensor digitorum communis*, No. 92, Gadow and Selenka, 1891, p. 282. *Extensor digitorum communis*, Fisher, 1946, p. 592.

Description (for the crow and raven; figs. 1, 2, 7, 25-31).—This is the middle muscle of the dorsal extensor group of the forearm. It originates by a short tendon from the Epicon. lat. hum. between the insertion of the Propat. b. proximally and the humeral origin of the E. car. ul. distally (fig. 11). The fusiform belly extends to about the middle of the forearm and beyond this the tendon runs distally in the space between the radius and ulna just anterior to the tendon of the E. car. ul. Near the wrist joint the tendon passes around the anterior surface of a small tubercle on the dorso-anterior side of the ulna in company with the tendon of the E. car. ul. It then crosses to the dorso-anterior surface of Meta. II, passes around the anterior side of a small tubercle near the base of the pollex, and bifurcates. A short branch inserts on the dorso-proximal end of the pollex and the main tendon extends distally in a well-defined groove along the antero-dorsal side of Meta. II to its insertion on the anterior side of the base of Phal. I, Dig. II (figs. 11, 18a, 19, 20e). Shortly before inserting the tendon turns abruptly ventrad and encloses a small sesamoid.

Action.—Extension of the hand, together with elevation of the pollex. Also tends to supinate the index digit.

Innervation.—A branch of the *N. radialis*, Gadow and Selenka, 1891, p. 283. A branch of the "post radial" branch of the *N. brachialis longus superior*, Fisher, 1946, p. 593.

Comparison.—In most forms examined the belly ends midway the forearm or slightly beyond. The belly ends somewhat farther distally in *Aphelocoma*, *Gymnorhinus* and *Cyanolyca*. The small sesamoid located in the tendon just proximad to the insertion is absent in most specimens, including immature ravens and crows. It was clearly present only in adult crows and ravens and in one *Psilorhinus*. It appears possible that in some

corvids this structure never develops, since it was absent in six specimens of *Nucifraga* that were known to be at least thirty-three months old.

M. EXTENSOR CARPI ULNARIS (E. car. ul.)

Flexor metacarpi radialis, No. 76, Shufeldt, 1890, p. 128. *Extensor metacarpi ulnaris*, No. 89, Gadow and Selenka, 1891, p. 276. *Flexor metacarpi radialis*, Fisher, 1946, p. 593.

Description (for the crow and raven; figs. 1-3, 5, 25-30).—This superficial muscle is located on the dorsal side of the forearm between the E. dig. com. and the anconaeus. It arises by two short tendinous heads, one from the Epicon. lat. hum. between the points of attachment of the E. dig. com. and the anconaeus, and one from the dorsal surface of the proximal end of the ulna just distal to the olecranon (figs. 11, 16b, 17b). The E. car. ul. extends along the dorso-anterior side of the ulna. The belly terminates at about the base of the distal third of the forearm. At the distal end of the ulna the tendon passes through a deep groove just anterior to a small bony tubercle which helps to hold it in place. Beyond this tubercle the tendon turns postero-distally over the dorsal surface of the ulna and the *Os ulnare* to its insertion on the postero-dorsal projection of the proximal portion of the carpometacarpus (figs. 11, 18d).

Action.—Flexion of the hand when the wing is extended; also elevation of the distal end of the wing. As indicated by Gadow and Selenka (1891, p. 277), this muscle belongs to the extensor group but due to the peculiar structure of the wrist and adjacent parts in birds it has secondarily assumed a flexor function.

Innervation.—A branch of the *N. radialis*, Gadow and Selenka, 1891, p. 277. Branches of the anterior branch of the *N. brachialis longus superior*, Fisher, 1946, p. 593.

Comparison.—Very uniformly developed. In *Cyanocorax* the belly extends along about the proximal three-fourths of the forearm; about four-fifths in *Calocitta*. In all others the belly is confined to about the proximal two-thirds.
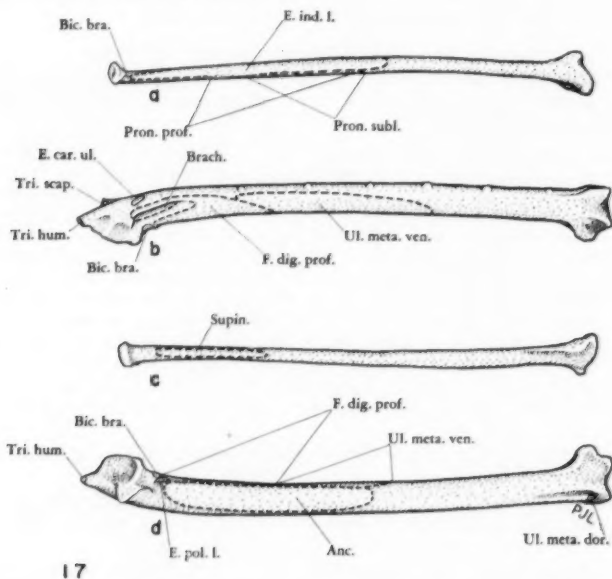
Fig. 17.—Crow. Bones of forearm showing muscle attachments. ×9.—a. Posterior surface of radius; b. Posterior surface of ulna; c. Anterior surface of radius; d. Anterior surface of ulna.

M. ANCONAEUS (Anc.)

Anconeus, No. 80, Shufeldt, 1890, p. 134. *Ectepicondylo-ulnaris,* No. 83, Gadow and Selenka, 1891, p. 268. *Anconaeus,* Burt, 1930, p. 494. *Anconeus,* Fisher, 1946, p. 595.

Description (for the crow and raven; figs. 1, 2, 7, 25-27).—This deeply situated muscle of the dorsal side of the forearm is almost entirely concealed by the more superficial E. dig. com. and E. car. ul. Origin is by a short tendon from the Epicon. lat. hum., between the humeral origin of the E. car. ul. and the joint capsule of the elbow (figs. 11, 16a). Insertion is fleshy on a very extensive area on the antero-dorsal surface of a little more than the proximal half of the Corp. ul. (figs. 11, 12, 17d). The ventral edge of the area of insertion is adjacent to the origins of the F. dig. prof. and the Ul. meta. ven.

Action.—Tends to elevate the distal end of the wing, together with a slight flexing motion.

Innervation.—A branch of the *N. radialis,* Gadow and Selenka, 1891, p. 269. Two branches of the *N. brachialis longus superior,* Fisher, 1946, p. 595.

Comparison.—Similar in all forms examined.

M. EXTENSOR POLLICIS LONGUS (E. pol. l.)

Extensor ossis metacarpi pollicis, No. 79, Shufeldt, 1890, p. 132. *Extensor pollicis longus,* No. 93, Gadow and Selenka, 1891, p. 283. *Extensor pollicis longus,* Fisher, 1946, p. 595.

Description (for the crow and raven; figs. 2-4, 7, 26-29).—This is an extremely small muscle lying ventral to the interosseous membrane connecting the radius and ulna, and posterior to the E. ind. l. It arises fleshy from a small area on the ventro-anterior surface of the proximal end of the ulna between the F. dig. prof. and the anconaeus (figs. 12, 17d). The belly is about one-third the length of the forearm. The minute, thread-like tendon extends distally along the dorsal side of the E. ind. l. Distally it lies along the posterior edge of the tendon of the E. meta. rad. to which it is closely attached before inserting on the antero-dorsal surface of Meta. I (figs. 11, 20b).

From the dorsal side the E. pol. l. is exposed upon removal of the E. dig. com., the E. car. ul., the Anconaeus, and the interosseous membrane.

Action.—Assists the E. meta. rad. in extending the hand.

Innervation.—Through a branch of the *N. radialis,* Gadow and Selenka, 1891, p. 286. Twigs from the anterior branch of the *N. brachialis longus superior,* Fisher, 1946, p. 595.

Comparison.—Very little differentiation was noted in this muscle. In most forms the belly is confined to about the proximal one-fifths of the forearm. In one specimen of *Aphelocoma coerulescens californica,* in one *Pica,* in *Garrulus, Calocitta* and *Cyanolyca* the belly extends almost midway the forearm. The specimen of *Garrulus* examined is peculiar in that the origin, in addition to the normal attachment to the ulna, is also connected to a small area near the proximal end of the radius.

M. EXTENSOR INDICIS LONGUS (E. ind. l.)

Extensor indicis longus, No. 81, Shufeldt, 1890, p. 135. *Extensor indicis longus,* No. 94, Gadow and Selenka, 1891, p. 285. *Extensor indicis longus* and *flexor metacarpi brevis,* Fisher, 1946, pp. 597, 601.

Description (for the crow and raven; figs. 1-5, 7, 26-32).—The single head of the E. ind. l. has a fleshy origin along the proximal three-fifths to two-thirds of the posterior surface of the radius, beginning proximally at the Tuber. rad. (figs. 11, 17a). The tendon extends distally in the space between the radius and ulna just ventral to the tendon of the E. dig. com. At the wrist joint the tendon runs around the anterior side of the ulna and continues over the dorsal side of the carpometacarpus. Beyond the middle of this bone the tendon passes along the anterior side of Meta. II and Phal. I, Dig. II to its insertion on the anterior side of the proximal end of the second phalanx (figs. 11, 20d).

Ventrally the E. ind. l. is exposed along the posterior side of the radius after removal of the Pron. prof. and Pron. subl.

Action.—Extension of digit II and the hand. Also tends to elevate the distal end of the wing.

Innervation.—Through a branch of the *N. radialis,* Gadow and Selenka, 1891, p. 286. From the anterior branch of the *N. brachialis longus superior,* Fisher, 1946, pp. 597 and 602.

Comparison.—In most specimens the belly of this muscle ends at about the proximal end of the distal third of the forearm. It is a little shorter in *Perisoreus* and somewhat longer in *Cyanolyca* and some specimens of *Aphelocoma.*

A unilateral variation was noted in the specimen of *Cyanocorax.* On the left side the
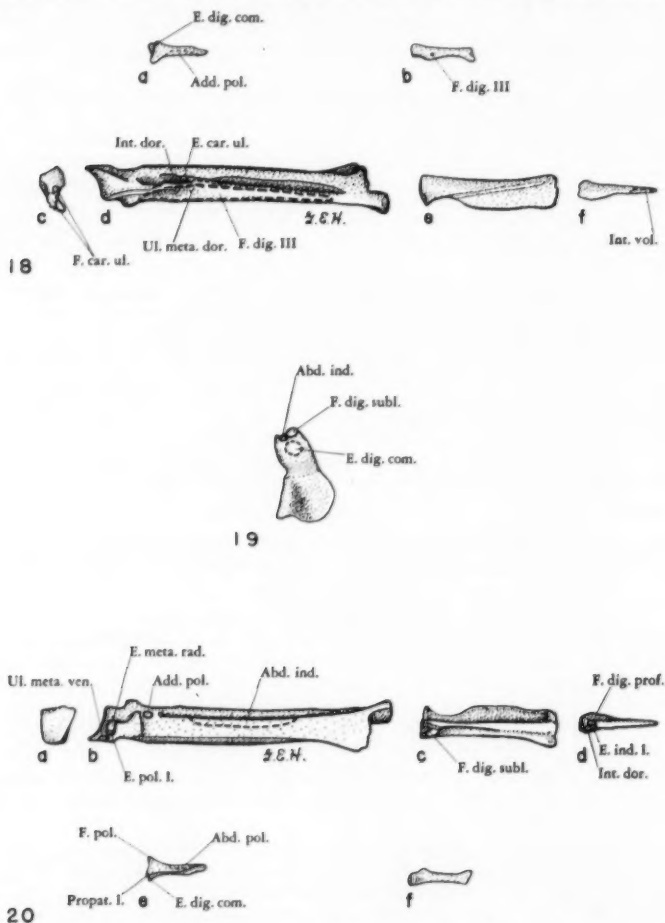
Figs. 18-20. Crow.—18. Posterior view of wrist and hand bones showing muscle attachments.—a. Pollex; b. Dig. III; c. ulnare; d. carpometacarpus; e. Phal. I, Dig. II; f. Phal. II, Dig. II. ×.9; 19. Proximal surface of Phal. I, Dig. II, showing muscle attachments. ×2.2; 20. Anterior view of wrist and hand bones showing muscle attachments.—a.—Ulnare; b. carpometacarpus; c. Phal. I, Dig. II; d. Phal. II, Dig. II; e. pollex; f. Dig. III. ×.9.

origin is from the radius only, as usual, but on the right side there is a distinct extra head of origin from the ulna. In one specimen of *Aphelocoma coerulescens californica* both sides have an extensive ulnar attachment.

In many birds, e.g., falcons, the E. ind. l. has a short distal head which arises from the dorsal side of the wrist joint and unites with the long tendon opposite the pollex (fig. 33). This distal portion is called the *Flexor metacarpi brevis* by Fisher (1946).

M. ULNIMETACARPALIS DORSALIS (Ul. meta. dor.)

Ulni-metacarpalis dorsalis, No. 87, Gadow and Selenka, 1891, p. 273. *Flexor metacarpi posterior*, Fisher, 1946, p. 605.

Description (for the crow and raven; figs. 2, 7, 30).—A short, weak superficial muscle located on the dorso-posterior side of the wrist joint. It arises by a strong tendon from the dorsal surface of the distal end of the ulna (fig. 11). The slender belly extends distally,
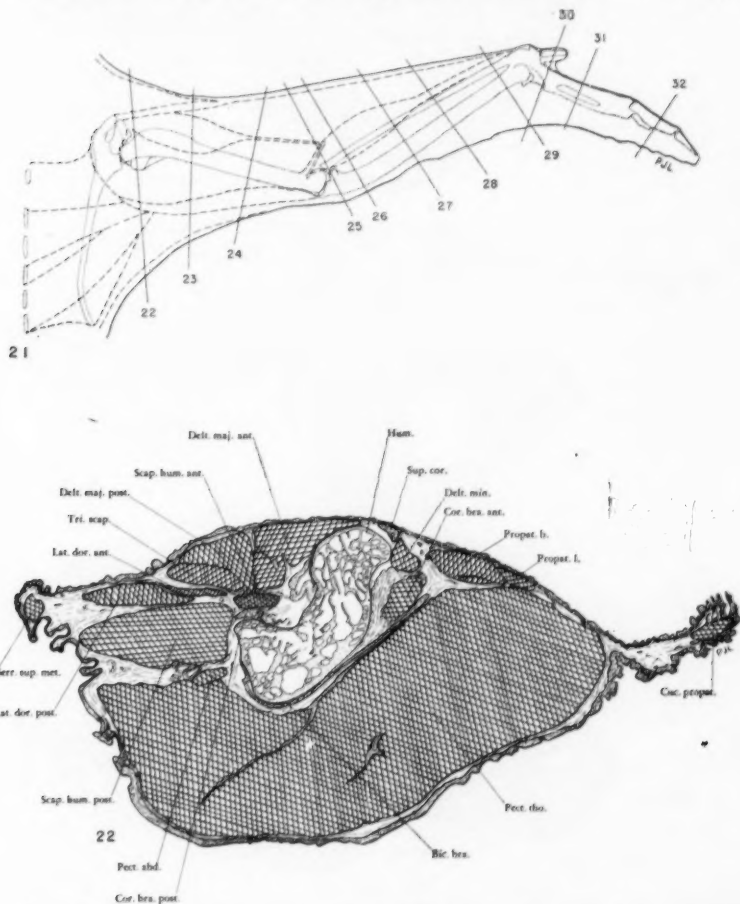
Figs. 21, 22. Crow.—21. Diagram of right wing, giving locations of cross sections shown in figs. 22-32. ×.4; 22. Cross section of brachium taken near extreme proximal end. Feathers removed. ×1.9.

adjacent to the posterior side of the tendon of the E. car. ul., to its fleshy insertion on the postero-proximal side of Meta. II, close to the insertion of the E. car. ul. and adjacent to the dorsal side of the belly of the F. dig. III (figs. 12, 18d).

Action.—Elevation of the hand, together with a flexing motion. In birds having attachments on primary quills the contraction of this muscle spreads the primaries when the wing is extended.
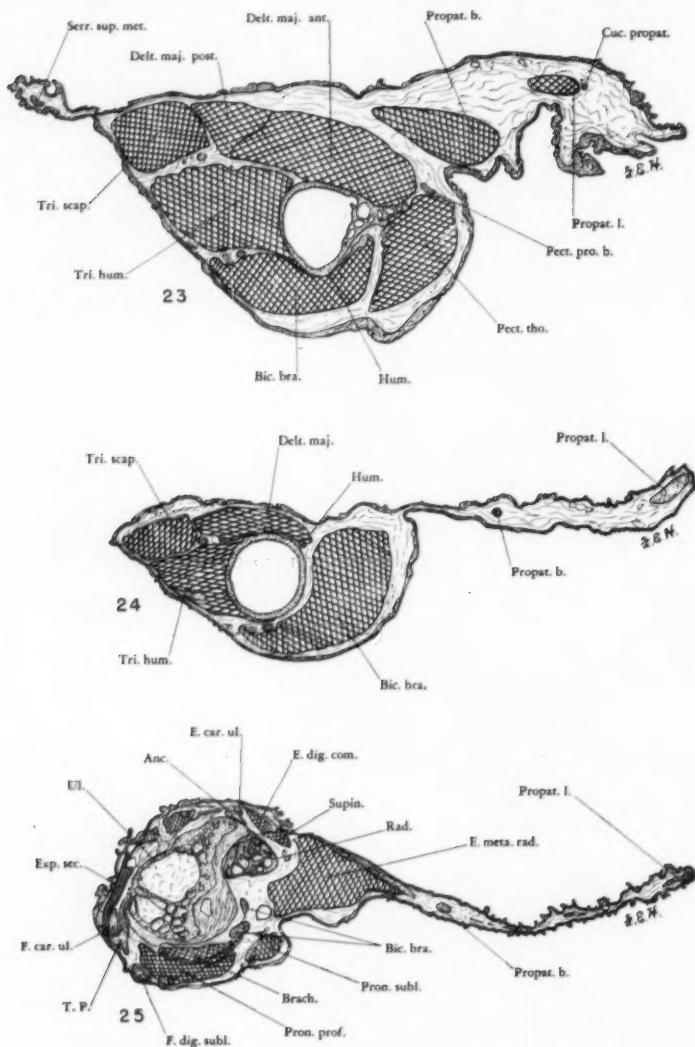
Figs. 23-25. Crow. Cross sections of wing. ×2.—23. End of proximal third of brachium; 24. Proximal end of distal third of brachium; 25. Extreme proximal end of forearm. T.P. = tendinous pulley.

Innervation.—Through a branch of the *N. radialis*, Gadow and Selenka, 1891, p. 274. From the posterior branch of the *N. brachialis longus superior*, Fisher, 1946, p. 605.

Comparison.—Similar in all corvids examined. In many birds the muscle is much larger and the insertion far more extensive than in the Corvidae. In *Falco mexicanus*, for example, the insertion includes much of the postero-proximal portion of Meta. III, besides attachments to several primary quills (fig. 33).
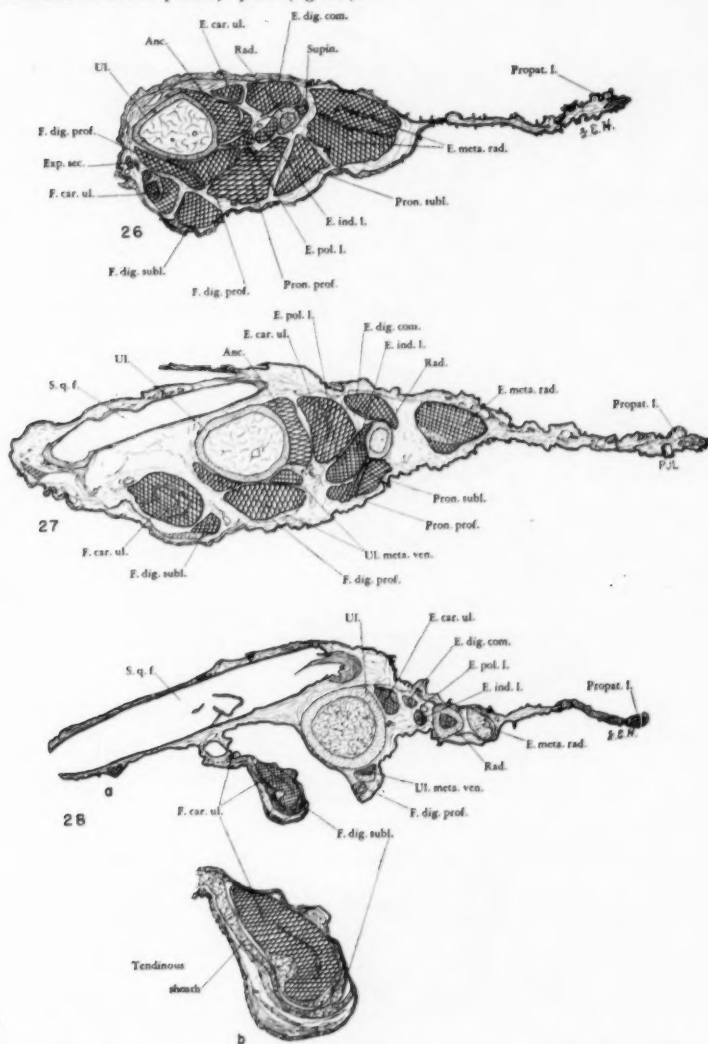
Figs. 26-28. Crow. Cross sections of forearm. S.q.f. = secondary quill follicle.— 26. Distal end of proximal sixth. ×1.8; 27. Two-fifths of the way from elbow to wrist. ×2.5; 28.—a. Three-fifths of the way from elbow to wrist.×2.5; b. Enlarged view of F. car. ul. and F. dig. subl. with surrounding sheath. ×6.2.

M. ABDUCTOR POLLICIS (Abd. pol.)

Extensor proprius pollicis, No. 85, Shufeldt, 1890, p. 147. *Abductor pollicis*, No. 98, Gadow and Selenka, 1891, p. 289. *Abductor pollicis*, Fisher, 1946, p. 600.

Description (for the crow and raven; figs. 5-7).—This small superficial muscle has a fleshy origin from the ventral surface of the distal end of the tendon of the E. meta. rad.
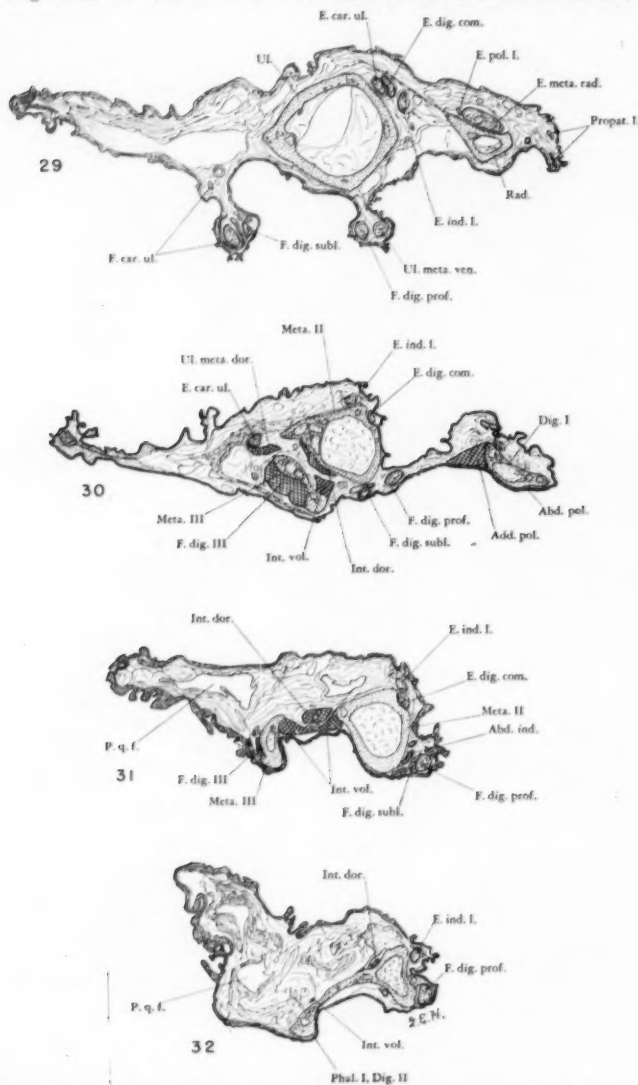
Figs. 29-32. Crow. Cross sections of forearm and hand. ×3. P.q.f. = primary quill follicle.—29. Proximal end of distal fifth of forearm; 30. Proximal end of hand at level of pollex; 31. About midway the carpometacarpus; 32. About midway Phal. I, Dig. II.

It inserts by a short tendon upon the ventral surface of the pollex, mainly at a point slightly proximal to the middle of the bone; however, tendinous fibers generally run out beyond this point (figs. 12, 20e).

Action.—Extension and depression of the pollex. This muscle also functions to a certain extent as a tendon of insertion of the E. meta. rad.

Innervation.—Through a branch of the *N. medio-ulnaris*, Gadow and Selenka, 1891, p. 289. From the anterior branch of the *N. brachialis longus inferior*, Fisher, 1946, p. 600.

Comparison.—Very similar in all species studied. In *Perisoreus, Cyanocitta, Cyanolyca, Aphelocoma ultramarina*, and some *Aphelocoma coerulescens*, the tendon terminates abruptly at the insertion, a little short of the middle of the pollex. In all other specimens more or less tendinous fibers insert farther distally.

M. flexor pollicis (F. pol.)

Flexor pollicis, No. 97, Gadow and Selenka, 1891, p. 288. *Flexor pollicis*, Fisher, 1946, p. 604.

Description (for the crow and raven; figs. 6, 7).—This minute muscle, when present, arises from the ventro-proximal surface of the carpometacarpus, anterior to the F. dig. prof. tendon at the point where the latter wraps around the Tuber. musc. meta. It inserts by a short tendon on the basal process of the ventro-posterior surface of the pollex (figs. 12, 20e).

Out of 22 wings of the crow and six of the raven we have been able to find the F. pol. in only two crow wings.

Action.—Depression and flexion of the pollex.

Innervation.—Through the *N. medio-ulnaris*, Gadow and Selenka, 1891, p. 289. From the anterior branch of the *N. brachialis longus inferior*, Fisher, 1946, p. 604.

Comparison.—This minute muscle was clearly observed in only one crow wing, with a trace in another. It was not found in any other corvid studied.

M. adductor pollicis (Add. pol.)

Flexor brevis pollicis, No. 86, Shufeldt, 1890, p. 148. *Adductor pollicis*, No. 101, Gadow and Selenka, 1891, p. 291; Burt, 1930, p. 497. *Adductor pollicis*, Fisher, 1946, p. 600.

Description (for the crow and raven; figs. 1-3, 5, 30).—This small muscle arises fleshy from the antero-ventral surface of the base of Meta. II (fig. 20b) and inserts mostly fleshy over almost the entire posterior surface of the pollex and on the ventral side of the quills of the feathers of the alula (figs. 12, 18a).

Action.—Adducts thumb.

Innervation.—*N. radialis*, Gadow and Selenka, 1891, p. 292. From the anterior branch of the *N. brachialis longus inferior*, Fisher, 1946, p. 600.

Comparison.—No significant variations were noted in this muscle.

M. extensor pollicis brevis (E. pol. br.)

Extensor pollicis brevis, No. 100, Gadow and Selenka, 1891, p. 291. *Extensor pollicis brevis*, Fisher, 1946, p. 602.

Although this muscle is absent in the Corvidae it is present in many birds. In *Falco mexicanus* it arises fleshy from the dorso-proximal surface of Meta. I and II and inserts on the antero-proximal edge of the pollex (fig. 33).

Action.—Extension (abduction) and to a slight extent elevation of the pollex.

Innervation.—*N. radialis*, Gadow and Selenka, 1891, p. 291. From the anterior branch of the *N. brachialis longus superior*, Fisher, 1946, p. 603.

M. abductor indicis (Abd. ind.)

Abductor indicis, No. 96, Gadow and Selenka, 1891, p. 287; Burt, 1930, p. 498. *Abductor indicis*, Fisher, 1946, p. 603.

Description (for the crow and raven; figs. 3-7, 31).—This is a small inconspicuous

muscle occupying the antero-ventral surface of Meta. II, mostly concealed by the tendons of the F. dig. prof. and F. dig. subl. The fleshy origin usually extends from a point opposite the pollex to about the proximal end of the distal third of the carpometacarpus (figs. 12, 20b). The fine tendon, frequently accompanied by a few muscle fibers, inserts upon the anterior surface of the base of Phal. I, Dig. II, beneath the F. dig. subl. tendon (fig. 19).
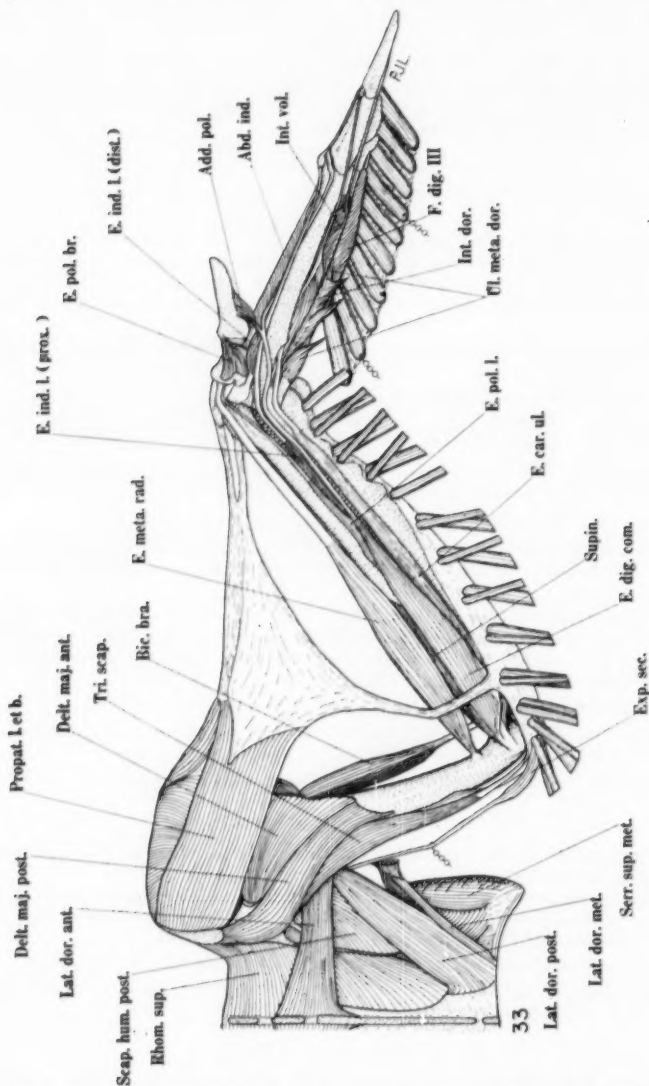
Fig. 33.—Prairie falcon (*Falco mexicanus*). Dorsal view of wing with skin removed. Primary quills reflected. ×,7.

Action.—Extension (abduction) of the index digit.

Innervation.—A branch of the *N. medianus,* Gadow and Selenka, 1891, p. 288. From the anterior branch of the *N. brachialis longus inferior,* Fisher, 1946, p. 603.

Comparison.—Similar in all forms studied. The belly is somewhat weaker in *Perisoreus* and *Cyanocitta* and is most strongly developed in *Calocitta.*

M. INTEROSSEUS DORSALIS (Int. dor.)

Interosseous dorsalis, No. 91, Shufeldt, 1890, p. 153. *Interosseus dorsalis,* No. 95, Gadow and Selenka, 1891, p. 286. *Interosseus dorsalis,* Fisher, 1946, p. 602.

Description (for the crow and raven; figs. 1-3, 6, 30-32).—The Int. dor. occupies the dorsal portion of the space between Meta. II and III, adjacent to the more ventrally situated Int. vol. The small bipinnate muscle arises fleshy from about the basal two-thirds of the intermetacarpal space, from the posterior surface of Meta. II, and the anterior surface of Meta. III. At the proximal end the muscle arises from the ventral surface of the fused metacarpals and to a slight extent from the dorsal surface (fig. 11). After crossing Meta. II and Phal. I, Dig. II, the tendon inserts on the antero-dorsal base of Phal. II, Dig. II (figs. 11, 20d).

Action.—Extension and elevation of the distal phalanx of the index digit.

Innervation.—A branch of the *N. medianus,* Gadow and Selenka, 1891, p. 287. From the anterior branch of the *N. brachialis longus superior,* Fisher, 1946, p. 602.

Comparison.—In most specimens studied the belly extends a little beyond the middle of the intermetacarpal space. In *Perisoreus* and *Cyanolyca* the belly ends about midway the space and in *Kitta* it is still shorter. In *Calocitta* the belly terminates at the proximal end of the distal one-fourth of the intermetacarpal space.

M. INTEROSSEUS VOLARIS (Int. vol.)

Interosseous palmaris, No. 92, Shufeldt, 1890, p. 153. *Interosseus palmaris,* No. 99, Gadow and Selenka, 1891, p. 290. *Interosseus palmaris,* Fisher, 1946, p. 602. *Interosseus solaris,* BNA (See Emmel, 1927).

Description (for the crow and raven; figs. 1-3, 5, 30-32).—This bipinnate muscle is immediately ventral to the Int. dor. It arises from about the proximal two-thirds of the borders of Meta. II and III where these bones enclose an interosseal space, from the posterior surface of Meta. II and the anterior surface of Meta. III (figs. 11, 12). The small tendon passes over the dorsal surface of Dig. III and crosses the posterior edge of Phal. I, Dig. II, to insert on the distal portion of the posterior edge of Phal. II, Dig. II (figs. 11, 18f).

Action.—Moves the distal end of Phal. II, Dig. II posteriorly, with slight elevation.

Innervation.—A branch of the *N. radialis,* Gadow and Selenka, 1891, p. 290. From the anterior branch of the *N. brachialis longus superior,* Fisher, 1946, p. 602.

Comparison.—In most specimens the belly of the Int. vol. extends along about the proximal two-thirds of the intermetacarpal space. It is somewhat shorter, about one- half, in *Perisoreus* and *Cyanolyca.*

M. FLEXOR DIGITI III (F. dig. III)

Flexor minimi digiti, No. 87, Shufeldt, 1890, p. 148. *Flexor digiti III,* No. 102, Gadow and Selenka, 1891, p. 292. *Flexor digiti III,* Fisher, 1946, p. 600.

Description (for the crow and raven; figs. 1-3, 6, 7, 30, 31).—The F. dig. III arises fleshy from the posterior border of Meta. III, receiving fine fibers from almost the entire length of this bone (figs. 12, 18d). The minute tendon inserts on the proximal tubercle on the posterior side of Dig. III (figs. 11, 12, 18b).

Action.—Tends to move the distal end of the wing posteriorly.

Innervation.—*N. radialis,* Gadow and Selenka, 1891, p. 214. From the middle branch of the *N. brachialis longus inferior,* Fisher, 1946, p. 601.

Comparison.—Similar in all forms examined.

SUMMARY AND CONCLUSIONS

In regard to the musculature of the wing the Corvidae studied show a remarkable uniformity. The small differences noted do not suggest any taxonomic groupings.
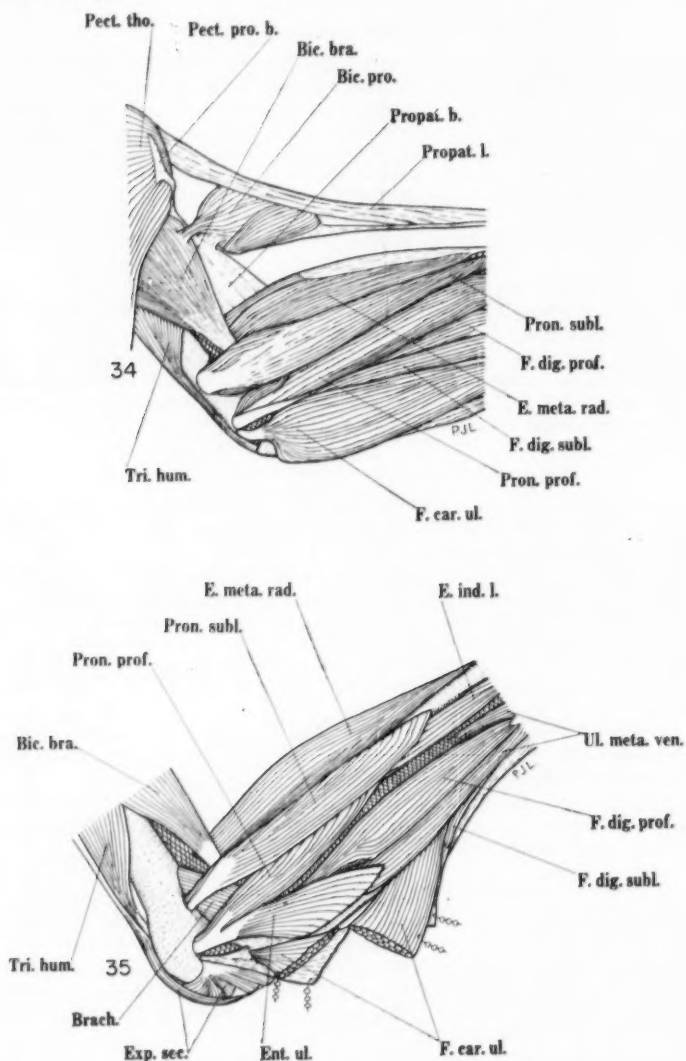
Figs. 34, 35.—34. Band-tailed pigeon (*Columba fasciata*). Ventral view of elbow region showing the biceps propatagialis. ×1.1; 35. Blue grouse (*Dendragapus obscurus*). Ventral view of proximal forearm, showing the entepicondylo-ulnaris. ×.9.

The following muscles or parts present in many birds were not found in the Corvidae: latissimus dorsi metapatagialis, biceps propatagialis, entepicondylo-ulnaris, extensor pollicis brevis and the distal head of the extensor indicis longus. The flexor pollicis was clearly observed in only one crow wing, suggesting that this muscle is in the process of disappearing in the Corvidae.

Modifications given for the various genera and species examined apply only to specimens listed under material and methods.

We would like to emphasize the desirability of stabilization in nomenclature of bird muscles and to deplore the coining of names simply because the muscles have not been properly identified. The following muscle names should be dropped from the literature since they represent either portions of well-known muscles or ligaments: flexor metacarpi brevis, abductor indicis brevis, flexor minimi digiti brevis, flexor brevis digiti III, and abductor minimi digiti.

In our opinion the digits of the bird wing should be considered numbers one, two, and three unless more conclusive evidence is offered from the field of embryology to prove that this is erroneous. If these digits are to be considered two, three and four, in addition to the changes in terminology of bones, the following in the names of muscles become necessary.

PRESENT NAME	CHANGE TO
Extensor pollicis longus	Extensor indicis longus
Extensor indicis longus	Extensor medius longus
Abductor pollicis	Abductor indicis
Flexor pollicis	Flexor indicis
Adductor pollicis	Adductor indicis
Extensor pollicis brevis	Extensor indicis brevis
Abductor indicis	Abductor medius
Flexor digiti III	Flexor digiti IV

There is a real need for a comprehensive study of the innervations of bird muscles, especially from the standpoint of homologies. Such investigations should include examples of many taxonomic groups in order to firmly establish homologies.

The study of the functioning of bird muscles is practically a virgin field and almost all of the work done to date has been on the basis of examining dead specimens. Further understanding of this subject will require carefully controlled experiments involving the transection and removal of muscles, electrical stimulation and other modern techniques in living birds.

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Some Factors Affecting Nesting Success of the Bob-white Quail in East-Central Texas

Paul W. Parmalee

Illinois State Museum, Springfield, Illinois

Locally bob-white (*Colinus virginianus*) abundance is controlled by conditions within the immediate habitat, primarily adequate food and cover, although a large number of additional factors are continually affecting quail numbers to a somewhat lesser degree. Geographically, bob-whites appear to be limited by extremes in temperature and precipitation and by such factors that accompany each of these conditions. Climate, in addition to its geographic influence, is of such significance as to produce periodic or seasonal fluctuations in quail numbers in regions where bob-whites have successfully established themselves and are filling a particular ecological niche. The influence of climate on bob-white populations in the post oak region during 1950 and 1951 has become evident from data based on temperature and precipitation records, nesting successes, and sex and age ratios.

THE POST OAK REGION

The post oak, black-jack oak climax represents an area comprising all or part of approximately 36 counties in east-central Texas. The topsoil is mostly a loose, light-colored sandy loam which often supports, in addition to the post and black-jack oaks (*Quercus stellata* and *Q. marilandica*), hackberry (*Celtis occidentalis*), water oak (*Quercus nigra*), pecan (*Hicoria pecan*), hickory (*Hicoria* spp.), an understory or thickets of yaupon (*Ilex* spp.), dogwood (*Cornus* spp.), winged elm (*Ulmus alata*), plum (*Prunus mexicana*), and stretchberry (*Smilax bona-nox*).

Although large tracts of the post oak region have been cleared for cultivation and pasture during the last 25 to 30 years, much of this cleared area is now being reclaimed by brush and woody species. This increased amount of brush and rather lax farming methods have provided additional suitable habitat for the bob-white. During 1950 and 1951 an ecological study was carried on in the post oak region, and such aspects of the quail's life history as nesting, movement, food and cover relationships, predation, parasites, and hunting pressure were considered.

Cooperating were the Texas Game and Fish Commission, the Texas Co-operative Wildlife Unit, the Wildlife Management Institute, and the U.S. Fish and Wildlife Service.

SPRING BREAK UP, COVEY DISPERSAL

The first "bob-white" calls were heard on April 1, 1950, and on March 31, 1951. The number of calling males increased rapidly during the last two weeks in April and reached a maximum, both in number and in intensity, in May. Field observations established the second and third weeks in April (1950, 1951) as the period of covey dispersal and pairing. As the tempera-

ture increased, the winter covey range was gradually abandoned. At first, the coveys broke up into groups of four and five birds that moved out into the roadsides, more open pastures, and along fence rows. By May 1 pairing had been completed.

Klimstra (1950) considered the distribution of pairs in Iowa as influenced by at least five factors: 1) A wide-spread improvement in cover which accompanied the progression of the nesting season. 2) The absence of a need of the small breeding populations for an immediate wide dispersal of pairs. 3) A shift of pairs to new localities which followed nest destruction. 4) The areas used for nesting are regulated, to a certain degree, by the locations of winter covey territories. 5) The distribution of pairs is influenced by suitable nesting habitat.

In the post oak region of Texas similarities and dissimilarities became apparent in comparison with spring dispersal of pairs in northern bob-whites as observed by Klimstra. Although grass and other succulent vegetation are reduced here during the winter months, reduction is never so complete as it is in the northern states, primarily because a milder winter climate is normally without lasting periods of ice and snow. As bob-whites pair off in the spring, nesting apparently is not delayed or greatly influenced by changes brought about in the vegetation density. Early nesting birds, therefore, utilize nesting cover produced during winter or retained from the preceding year. When nesting cover is plentiful, principally because of a wet fall and winter season, the degree of nesting success is high. Without a winter holdover of cover that can be utilized by nesting birds the following spring, the nesting season is less successful.

Factors two and four as set forth by Klimstra apparently apply to this region. Quail populations are at their lowest density in the spring, and the amount of suitable nesting cover seems sufficient to accommodate the number of potential nesting pairs present. However, bob-whites do not always use what can be considered good cover even when it is available. Dispersal is widespread during the summer months, but there appears to be a rough correlation between winter covey range and the general location of summer pairs. Data to substantiate this conclusion definitely were not available for this region, but such a correlation was reported by Lehmann (1946) for bob-whites in south Texas.

Factor three, as determined by Klimstra, may not apply as a general rule in the post oak region. During the summers of 1950, 1951, pairs of quail without young were observed at approximately the same site throughout the summer. Presumably the pairs were the original birds observed since they could be seen, particularly in the late evening, in the same general locality. It is not known whether these birds had attempted to nest.

The last factor considered by Klimstra is apparently operative for the bob-white in all parts of its range. The majority of quail in this area utilized pasture or grassland of one form or another for nesting, although brush and woodlands were also used to a limited extent. Normally quail tend to avoid the more wooded sections and to nest in open or semi-open fields and pastures.

LOCATING NESTS

The thick grass cover present in the spring of 1950 afforded bob-whites

an unlimited amount of excellent nesting cover. Numerous methods were employed to locate nests, but no one method was found more satisfactory than another. In the first efforts to find nests, a detachable flushing bar, similar to one described by Lehmann (1946), was used extensively. However, obstacles such as rough or wet pasture and the interference of brush and other vegetation often prevented successful operation of the bar. Also, it was felt that sections of 30 inch chain (and their weights) that were suspended at two-foot intervals on the bar, were not effective in flushing an incubating parent from a nest that might have been between the lengths of a chain.

Nests found by the writer were located by walking or driving over areas that appeared to be good nesting sites and where pairs had been observed. A bounty of fifty cents was also offered for any nests located, and this resulted in the finding of several nests by Negro tenants living in the vicinity of the two main research areas (640 acres each) in Robertson County. In the spring of 1951, members of the Brazos County Highway Department were contacted and, through the cooperation of those operating the mowing equipment, several additional nests were discovered.

DETERMINATION OF NESTING SUCCESS

In an effort to determine nesting success in the central post oak region during the spring and summer of 1951, double post cards were sent to landowners in 13 counties within this area requesting information regarding nests found by them. Ten representatives from the Soil Conservation Service, 15 from the Production and Marketing Administration, and 15 county agricultural agents were first contacted by letter, informed briefly of the problem, and asked to submit names and addresses of 25 landowners in their respective counties whom they thought might cooperate.

Twenty-three agents returned the requested list of 25 names, and, after omitting duplications, 564 cards were sent out asking for the following information: Date nest was found; nest location—pasture, roadside, hay field, etc.; number of eggs in each nest; whether successful or destroyed; number of eggs that hatched, and if known, the reason for destruction of nests.

The card was so arranged that the above information could be entered for four or five nests. There was additional space for the landowner's name, his address, and the county in which he resided. Fifty-seven (10.1 per cent) of the cards were returned, the majority containing information on one or two nests, although several individuals noted that no nests were found. The data obtained from these cards, including nests examined by the author, are listed in tables 1 and 2.

RESULTS OF NESTING DATA SURVEY

Of the quail nests reported during the nesting season of 1951, 34 or 62.9 per cent were successful, representing an average-to-good hatch. Although no complete figures are available for the 1950 nesting season, the degree of hatch success appeared even greater. Numerous landowners reported finding many nests during May and June of 1950, of which a high percentage were known to have been successful.

Data submitted by landowners concerning the cause of nest failure were

TABLE 1.—Nesting data from 13 counties in the post oak region
of Texas. May, June, and July 1951

Number of nests located	59
Number of successful nests	34
Unsuccessful nests	20
(a) Abandoned	6
(b) Destroyed	14
Fate unknown	5
Average number of eggs per nest	12.9
Average number of eggs hatching per nest	11.9

TABLE 2.—Location of nest site, based on records of 61 quail nests from 13
counties in the post oak region. June, July, and August 1950 and 1951

Nest Site	Number of Nests	%
Open pastures, fields or meadows	22	36.1
Beside buildings	2	3.3
Fallow fields	3	4.9
Fields or pastures bordering roadsides	19	31.1
Fence rows in pastures	5	8.2
Cultivated fields	4	6.6
Oak woods—woods bordering roadsides	3	4.9
Thickets and underbrush	3	4.9
	61	100.0

not complete because of lack of exact information on the predator involved. However, nine of the abandoned or destroyed nests were the result of human interference, the losses being due primarily to mowing equipment. Apparently a high percentage of nests built along highways are abandoned after being uncovered and exposed by mowing crews. Four such nests discovered during mowing operations in Brazos County, Texas (two in June and two in August 1951), were abandoned. However, one nest in Brazos County containing 16 eggs uncovered in a like manner in June 1950, was not deserted. The hen was noted incubating on two return visits, and sometimes between the second and third visits the eggs hatched.

The average of 12.9 eggs per nest is slightly less than the average of 14.00-14.96 eggs for the years 1924-27 reported by Stoddard (1931). Lehmann (1946) noted averages of 14.8 eggs for early spring clutches, 11.5 in mid-summer nests, and 10.5 in late summer clutches. The figure of 12.9 represents the average number of eggs in successful nests during the entire nesting season of 1951. The largest number of eggs hatching from one nest was 23, the smallest 3.

Mr. E. A. Webster of Groesbeck, Texas, reported that for many years he has found single eggs, principally during May, in pathways, under bushes, and at various locations in fields near his home. Stoddard (1931) attributes this

TABLE 3.—Comparison between development of ovaries of immature
and adult quail during March, April, and May, 1951

	Adults		Immatures	
Date	Ovary size (mm)	Individual egg size	Ovary size (mm)	Individual egg size
3/30/51	14 x 8	All same size.	14 x 7	All same size.
4/19/51	18 x 11	16 of increased size. Largest 4 mm.		
4/25/51			15 x 7	4 of increased size. Largest 3 mm.
5/17/51			17 x 12	14 of slightly increased size: 4 mm. One enlarged egg: 10 mm.
5/24/51		Egg in cloaca: 30 x 23. Four enlarged ova: 19 x 16 16 x 13 11 x 9 7 x 7		

to hens that have had their nest destroyed during the laying period or to hens forced to lay before reaching the nests. The former explanation appears to be the more satisfactory in this case, since Webster noted an unusually high number of these eggs during May of 1951, at which time several clutches that he had found in the process of being completed were destroyed by some predator. Only one nest of seven found on his land in the spring of 1951 was successful.

During the opening week of the 1951-52 hunting season (December 1-7), three eggs were picked up in the field by Mr. Webster. These were examined and found to be fresh. A fourth fresh egg was collected by Mr. Webster during the first week of January 1952. On October 29, 1951, a fresh quail egg was taken from beneath a rose bush on the main study area. These eggs may have been laid by immature bob-whites (birds of the year) or by hens attempting late nests, but the exact reason remains a matter of speculation.

IMMATURE FEMALE QUAIL AS LATE NESTERS

Late nests are considered by most investigators to be a result of second or third attempts of a hen to renest after the first clutch is destroyed. Data regarding the development of eggs in adult (two years or older) and immature (birds of the preceding year) female bob-whites during March, April, and May establishes the possibility that immature hens, about to nest for the first time, may normally do so somewhat later in the season than adults (table 3).

The available data are not sufficient to establish this theory as fact; a larger number of adult and immature females, collected on the same date and periodically during this three-month period would be necessary to verify this assump-

tion. However, an adult female collected April 19, 1951, showed ovary development in advance of an immature female collected April 25, 1951. An adult female taken on May 25, 1951, was apparently in the process of completing a clutch of eggs, while ovary development in an immature female examined May 17, 1951, showed little advancement. An immature female shot August 18, 1951, had with her a brood of four 8-to-10-day-old chicks. This brood, however, may have been the result of a second nesting attempt.

LOCATION OF NEST SITES

Table 2 represents a summary of the various nest sites and the number of nests found in each, as recorded from data collected by landowners and the author. Approximately 85 per cent of the nests were located in pasture or grassland of some type, while the remaining 15 per cent were placed in miscellaneous locations. Petrides,* in summarizing 336 reports of farmers on quail nests from several counties in the post oak region, found the highest number of nests per 100 acres in pastures and hay fields. Although unusual nest sites were chosen, the majority of birds in the post oak region utilized the better grass cover along roadsides, in hay fields, and in pastures.

Fourteen nests (data included in tables 1 and 2) were examined by the author in the springs of 1950 and 1951. Twelve were located within 50 feet of a main highway, dirt path, or gravel road. There was apparently a strong tendency for birds to utilize roadsides, possibly because of the good cover they often provided. Stoddard (1931) observed this tendency in bob-whites in the Southeast when he noted that "more than 79 per cent of all nests studied in woodland and open country alike, were within 50 feet or less of such openings (roads, paths, etc.) while less than 19 per cent were more than 50 feet distant."

There also appears to be a tendency to nest under fences or along fence rows. Three nests discovered by the author and several others reported by landowners were so situated. Errington (1933) observed this in Wisconsin bob-whites and considers the possibility that the habit is an evolutionary tendency on the part of quail to nest in such places because they are protected from trampling and other destroying agencies.

Silver beardgrass, the dominant grass species along many of the highways, was utilized by several nesting quail. Perennial grasses, such as silver beardgrass and little bluestem, were especially important because of their resistance to drought and the rigors of winter. Species of vegetation used by the 14 nesting quail and the number of nests in each are as follows:

Silver beardgrass (*Andropogon saccharoides*)	3
Silver beardgrass & needlegrass (*Stipa leucotricha*)	3
Needlegrass	1
Silver beardgrass & little bluestem (*Andropogon scoparius*)	1
Little bluestem & greenbrier (*Smilax* sp.)	1
Silver beardgrass, greenbrier & winged elm (*Ulmus alata*)	1
Little bluestem	1
Ryegrass (*Elymus* sp.)	1
Bull grass (*Paspalum* sp.)	1
Brownseed paspalum (*Paspalum plicatum*) & dewberry (*Rubus* sp.)	1

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* Data collected while Unit Leader, Texas Cooperative Wildlife Unit, Agricultural and Mechanical College of Texas, 1950.

All of the 14 nests except one fell into the classes of "Much" (nests very difficult to see even when exact location is known) or "Medium" (fairly easily seen if location is known) set up by Stoddard (1931) in regard to quantity of concealing vegetation. All nests except two that were located in roadside ditches were well situated in regard to drainage. The entrances to 9 of the 14 nests faced a south, southeast, or southwest direction. The number of nests for which this datum was recorded is insufficient to justify a definite conclusion on entrance direction, but is, in all probability, not significant since Stoddard (1931) found that "nests are as likely to face toward one point of the compass as another, there being no noticeable preference in this respect."

SEX AND AGE RATIOS

Criteria for separating young of the year from adult bob-whites have proved valuable in determining the significance of climate and other ecological factors influencing quail numbers for a given season or habitat. Many investigators, Stoddard (1931) being one of the first, have pointed out that quail shooting is non-selective, and that the age and sex composition found in a representative sample killed by hunters may be considered the same as those existing in the population. Leopold (1939) was the first to describe fully the differences in wing plumage by which bob-whites of the year could be distinguished from older or adult birds. Since that time, several writers, notably Petrides (1942), Petrides and Nestler (1943), and Thompson and Kabat (1950), have added to and improved upon this aging technique based on plumage molt.

Color and color pattern differences between male and female bob-whites make it a simple matter to distinguish the sexes. This method has been of prime significance in obtaining sex and age data on a large scale. About one month before the start of the quail season (December 1 to January 16) local hunters were contacted and asked to save one wing from each quail killed, the right from males and the left from females. Envelopes were supplied to each hunter so that wings collected on various hunts could be kept separate and the date, county in which the birds were killed, and the name of the hunter were written on the envelope.

Table 4 represents the adult-immature ratios as determined by wings submitted during the hunting seasons of 1949-1950, 1950-1951, and 1951-1952. Table 5 presents the summary of hatching dates of immature birds collected during the 1949-1950, 1950-1951, and 1951-1952 hunting seasons. These data, correlated with field observations and climatological records, tend to clarify the conditions that in part affected quail populations in this region during the last three years.

CLIMATOLOGICAL DATA

Temperature and precipitation data were obtained from meteorological records of the Texas Agricultural Experimental Station at College Station, Brazos County, Texas. Variations in temperature and precipitation occurred at the more northern and southern extremes of the region and in small local areas, but these meteorological data represented satisfactorily the over-all weather conditions prevalent during 1949, 1950, and 1951 in the central portions of the post oak region of Texas.

Examination of the adult-juvenile ratio and hatching dates for juveniles in
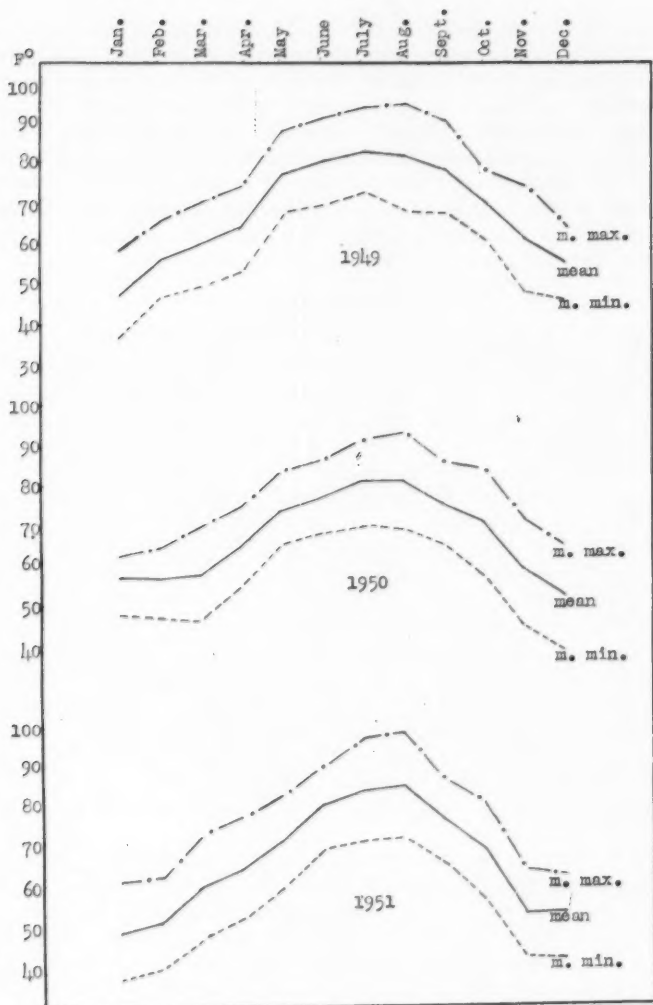
Fig. 1.—The monthly rainfall, in inches, recorded at College Station,
Brazos County, Texas, for the years 1949, 1950, and 1951

1949 indicated that bob-whites experienced a year of "average" reproductive
success. At a 1:1 adult sex ratio, only 4.96 young per adult female were
recorded in 1949, whereas 9.74 young per adult female were noted in a year
(1950) classified as "good" or even "excellent." As a contrast in 1951, 2.40
young per adult female represented either a poor hatch or a low immature
survival rate.

Fig. 1 illustrates the monthly rainfall for the years 1949, 1950, and 1951,

TABLE 4.—Adult-immature ratios as determined by quail wings
submitted during the hunting season

| | December 1 to January 16 | | |
	(143 Wings— 7 Counties) 1949-1950	(349 Wings— 13 Counties) 1950-1951	(553 Wings— 13 Counties) 1951-1952
Adults	41	51	246
Adult Females	23	15	110
Young	102	298	307
Young/adult	2.48	5.84	1.20
Adult Sex Ratio	1:1	2:1	1:1
Young/Adult Female	4.96	9.74	2.40

TABLE 5.—Summary of hatching dates for immature quail based
on wings submitted during the hunting season
December 1 to January 16

	1949-1950	1950-1951	1951-1952
Total Number of Young	102	298	307
Hatched Prior to Aug. 15	88 (86.3%)	286 (90.0%)	304 (98.9%)
Hatched After Aug. 15	14 (13.7%)	30 (10.0%)	3 (1.1%)

while fig. 2 presents the monthly mean, mean maximum, and mean minimum
temperatures experienced during these three years.

Although the rainfall in 1949 was normal, precipitation in 1948 was below
normal and reduced much of the available ground cover (grass and other suc-
culents). The rains during April 1949, improved cover conditions, enabling
the bob-whites to bring off many of the early and midsummer broods (86.3
per cent hatching prior to August 15). Apparently the survival rate of young
quail was only average.

The spring and summer of 1950 proved to be one of the best years in
regard to nesting success and survival of young. Data showed 9.75 young per
adult female, 90 per cent of the young hatching prior to August 15. Hunters
reported seeing more quail during the 1950-51 season than they had observed
during the past four years. Rainfall was heavy during the winter of 1949 and
the spring of 1950, and precipitation continued in April, May, and June. The
winter and early summer rains produced excellent stands of grass and other
herbaceous vegetation that provided good nesting cover as well as protection
for the young during the summer.

A serious drought, relieved only temporarily by rains in March, 1951, began
in July, 1950, and lasted until September, 1951. This condition, coupled with
extreme temperatures during both summers, reduced previously good summer
quail range to barren ground or fields of stubble. The March, 1951 rains,
however, did produce some new growth that helped provide many nesting birds
with suitable cover.

Examination of hatching dates of juvenal quail in the summer of 1951
showed that of the birds surviving to the hunting season, 98.9 per cent hatched
prior to August 15. Brood counts during July and August, 1951, indicated
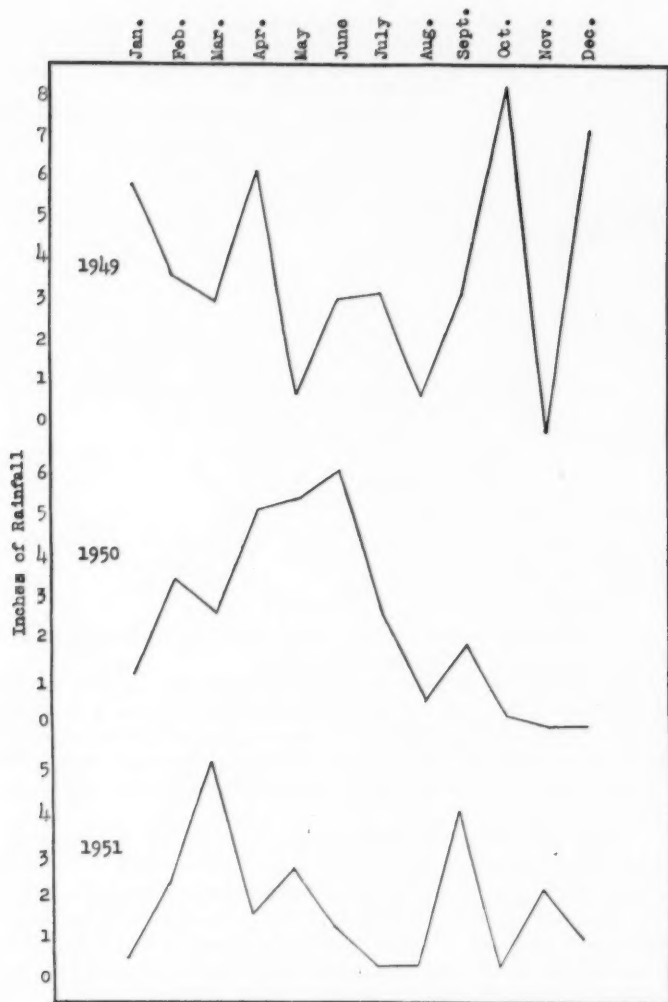
Fig. 2.—Monthly mean, mean maximum, and mean minimum temperatures recorded
at College Station, Brazos County, Texas, 1949, 1950, and 1951

small families (12 late broods averaged 8.9 birds). In addition, numerous
broods observed in July and August contained young chicks. One hen ob-
served August 18 had with her four chicks from three to five days old.

Several quail families under observation on or near the research areas during
the summer of 1951 showed a gradual reduction in number of young as the
season progressed. Many of the early nests were unsuccessful, and late broods
failed to increase the fall population because of an apparently high mortality

rate among them. Little cover was available for mid- and late summer nesting birds (as well as for young being reared at that time), and their chances of hatching and rearing broods were considerably reduced.

By comparing the available field and the climatological and sex and age ratio data for this three-year period, there appeared to be a definite correlation between nesting success and the attainment of maturity by the young on one hand and precipitation on the other. However, Lay (1949) indicated that breeding success seemed to be little affected by dry or wet years. He also stated that during the span of his quail project in east Texas, one of the "driest" years on record was experienced. Thirty-six inches of rainfall fell during this dry year; 36 inches is a normal yearly rainfall in the post oak region and when below-normal years occur, nesting apparently is seriously affected.

Lehmann (1946) considers weather, primarily rainfall, as one of the two outstanding important factors regulating bob-white reproduction in southwest Texas, the other factor being predation. It becomes apparent that as bob-whites extend their range into geographic regions only partially or periodically suited to the birds' requirements, population numbers tend to be unstable and noticeably influenced by several factors, particularly climate.

SUMMARY

Male bob-whites begin calling about April 1, and by May 1, pairing is completed. The amount and density of ground cover produced during the winter or retained from the preceding year is important in determining early spring nesting success.

Of the 59 quail nests recorded during the nesting season of 1951, 62.9 per cent were successful. Almost 80 per cent of the nests recorded were located in open pastures, fields, and meadows, or along grassy roadsides. The average number of eggs per clutch was 12.9.

Limited data indicate that juvenal females (birds of the preceding year) may normally nest later in the season than females two years or older in age.

A correlation of climatological data with adult-juvenile ratios and hatching dates of juvenal quail, indicates that with an average to heavy winter or early spring rainfall, a successful hatch and rearing season will usually result.

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Additional Observations of Birds and Mammals in the Vanderhoof Region, British Columbia

J. A. Munro

Okanagan Landing, British Columbia, Canada

Field work in the Vanderhoof region subsequent to the publication of my paper (Munro, J. A., The Birds and Mammals of the Vanderhoof Region, B.C., Amer. Midl. Nat. 41:3-138, 1949) has provided additional records of both birds and mammals. These, together with observations of recent mammal population trends, and studies of bird behaviour, seem to justify publication of this supplement.

BIRDS

Aquila chrysaetos (Linnaeus). Golden Eagle.—Recorded earlier on the basis of sight observations by local residents in winter. On June 13, 1952, a golden eagle was flushed from the ground beside the Lake District-Vanderhoof road. It was in the plumage of the second year. The eagle rose only high enough to clear the tree tops and alighted near the top of a spruce close to the road. A moment after it landed an adult female Cooper hawk, flying fast over the aspen tops, swooped down to it once, then passed quickly out of view.

Pedioecetes phasianellus (Linnaeus). Sharp-tailed Grouse.—From scarcity in 1945-46 the numbers increased annually to relative abundance in 1952, when the population in the Lakes District was estimated to be 500. In a series of 30 specimens collected in September —nine in 1950, 10 in 1951 and 11 in 1952, the proportion of young to adults was at a ratio of four to one.

These have been compared with series, in fresh fall plumage, from the Cariboo Parklands and the Okanagan Valley. The last, probably typical of *P. p. columbianus*, are palest of all on the dorsal surface, Vanderhoof specimens are the darkest and Cariboo specimens are intermediate. That is to say the series show a progressive darkening of dorsal plumage from south to north.

Ventrally, no appreciable difference between Okanagan Valley and Cariboo specimens is detected. In the Vanderhoof series, however, there is considerable darkening of this surface, the margin of individual feathers being wider and, in the majority, black, or nearly so, rather than dark umber as are Cariboo and Okanagan Valley specimens. Thus the pattern, black and white rather than brown and white, is a distinctive character. Possibly in this respect, as well as in the dark dorsal coloration, the Vanderhoof population is closer to *P. p. kennecottii* than to *P. p. columbianus*.

A day-old chick from the Vanderhoof region may be described as follows: ventral surface nearest to Amber Yellow, but the sheen of the down gives it a brighter, more golden cast; dorsal surface nearest to Sulphine Yellow, partly obscured by a prominent black pattern; upper mandible yellow-drab with median dusky stripe on basal half; lower mandible straw; iris olive-grey; toes pale yellow.

Several miles east of Nulki Lake a 20-acre field was cleared of aspens and brush in 1950 but not further cultivated, so that grasses, vetches, fireweed and other plants made vigorous growth. It is a favorite feeding ground for sharp-tailed grouse in autumn. Here on June 10, 1952, a female was flushed from a nest containing 13 eggs which later observations proved to be within 48 hours of hatching. In colour they were nearest to Ecru Drab profusely freckled with minute dusky spots. The nest cavity, eight inches in diameter, was in black loam and partly concealed by a tuft of grass and by fireweed *Epilobium* sp. 12 to 14 inches in height. This vegetation, that provided adequate cover during most of the incubation period, must have been much shorter and less effective in this respect during the laying period.

The female was on the nest at 10:00 a.m. on the following day, and did not flush when two of us stood for several minutes within six feet.

At 9:00 a.m., June 12, when I next visited the nest, and made several film exposures at four feet, the female remained on it motionless, but flushed when I put out my hand to touch her. It was seen then that six eggs had hatched. Several chicks began to scramble out of the nest and were put back, others still wet from egg moisture, remained inactive. Meanwhile the female walked about among the weeds a few feet away making a soft, crooning noise. At 2:00 p.m. three more eggs had hatched and, as before, the female when flushed walked through the vegetation never far from the nest; this time she dragged her wings on the ground.

At 11:30 a.m., June 13, all the eggs were hatched and the female was brooding the chicks. When she flushed the chicks, now dry and fluffy, ran out of the nest in all directions. On the morning of June 14 the nest was empty. The brood was not seen then nor later.

Totanus melanoleucus (Gmelin). Greater Yellow-legs.—A probable nesting was indicated by the actions of an adult at Manson's Slough on July 1, 1952. This bird followed, or preceded us, for half of the distance around the slough. It called continually, alighted on fence posts and acted in the excited manner common to this wader when defending young.

Otus asio (Linnaeus). Long-eared Owl.—On July 11, 1948, I called up by "squeaking," a long-eared owl at a place where one had been seen on August 16, 1946. This is the second definite record.

Dryocopus pileatus Linnaeus. Pileated Woodpecker.—A nest of this woodpecker containing large young was kept under daily observation from June 22 to June 30, 1952. The nesting tree was a live aspen, 12 inches in diameter at the base and without branches for 60 feet, one of four growing close together in a mixed forest of aspen, Douglas fir and Engelmann spruce. The nest entrance, four inches in widest diameter, was 40 feet above the ground. In the same tree were three other nest holes, with entrance of similar size, undoubtedly used in earlier years by pileated woodpeckers. Three were in nearly regular alignment, one five feet above, the other five feet below the occupied nest. The fourth was five feet below, and slightly to the right, of the lowest of the other three. These measurements are approximate.

The nest was first discovered on June 22 through seeing the female approach the nest in short flights from tree to tree, calling at short intervals. She entered the nest and quickly re-appeared carrying a faecal sac, to return and again enter the nest precisely 20 minutes later. These, and the following observations, were made while I stood about six feet from the base of the tree in full view. Neither adults nor young showed any concern at my presence.

At 11:30 a.m., June 23, when I walked to the bottom of the tree, the head of the female appeared at the nest entrance. She remained there several minutes with bill opened, then flew to a tree 100 yards distant and dressed her plumage.

At 9:00 a.m., June 24, one young about three-quarters grown was at the nest entrance with head and neck protruding. The bill opened and shut continually and the bird gave a series of soft notes, one following another in rapid succession, evidently a call for food. Numerous flies, possibly *Protocaliphora*, circled about the entrance and undoubtedly irritated the bird which continued shaking its head from side to side. Subsequently, except on one day when the temperature was low and no flies were present, this head-shaking was noted whenever a young bird occupied the nest entrance.

At 9:10 a.m. the female alighted in a spruce 50 feet or so from the nesting tree. Five minutes later she gave the familiar loud cackling call, and at once the heads of two other young appeared at the entrance. The female then flew directly to the nest and fed the young with rapid, downward thrusts of the bill. On this occasion she clung to the bark in such a position that the young were screened from my view. After she left the three young remained at the entrance, the head of the larger bird above those of the others, for 10 minutes, then the two smaller birds withdrew. The third continued to occupy the entrance for the 20 minutes I remained on watch. Sometimes its shoulders and breast were visible filling most of the entrance; again, it withdrew into the space behind the entrance where the circumference was greater, sufficient to permit the bird to dress its plumage and this it did vigorously.

At 4:00 p.m., June 26, the larger young was at the nest entrance and both parents were in nearby trees. Once the adults flew to a broken-topped aspen, one alighting on the break, the other two feet above. Here they performed what, no doubt, was part of the court-

ship display, assuming various striking attitudes with crests elevated to their full extent. Later the female flew to the spruce which she had used before and soon gave the regular call. The larger young, alone at the nest entrance with head turned at right angles as it watched the parent, gave the begging cry continually. When the female called another young showed its head. She flew to the nest and fed the two birds. This time she clung a little to one side of the entrance, not shielding the young from view as before and I could see how she thrust her bill deep into the throat of first one, then the other. After she left the third young appeared; three heads were visible for several minutes, then two were withdrawn.

At 5:00 p.m., June 30, one young was at the nest entrance while the adult female occupied the nest below, her head showing at its entrance for the five minutes she remained there. This observation suggested that possibly the older nests are used as night roosts by the adults. By the following morning both adults and young had left and evidently had travelled a considerable distance from the nesting territory for none was seen, nor were their voices heard, in the surrounding woods.

Asyndesmus lewis (Gray). Lewis Woodpecker.—A juvenile female in full moult was collected near Sinkut Lake, September 20, 1952; this constitutes the first record for the region. Also it is the third record of the species' occurrence far north of its normal range, the other localities being: Takla Lake, approximately 115 air-line miles northwest of Vanderhoof (Fletcher, J. F. S. and T. C., 1943. Occ. Papers B.C. Provincial Mus. No. 4, 1-97) and Masset, Queen Charlotte Islands (Munro and Cowan, 1947. A Review of the Bird Fauna of B.C. Spec. Pub. No. 2, B.C. Prov. Mus.).

Spyraphicus ruber (Gmelin). Red-breasted Sapsucker.—One of the commoner summer visitants in 1945 it was much less so in 1946. In subsequent years the population showed little or no increase from the 1946 level and in the summer of 1952 a total of only four individuals was recorded.

Parus rufescens Townsend. Chestnut-backed Chickadee.—Two specimens, birds of the year with incomplete skull granulations, were collected near Bradley's Slough, September 27, 1952. This is a new record for the region.

Troglodytes troglodytes Linnaeus. Winter Wren.—A male, showing incomplete skull granulation was collected on Sinkut Mountain, September 30, 1952. The subspecies is *T. t. pacificus* Baird. This represents the first local record for the species.

Ixoreus naevius (Gmelin). Varied Thrush.—An adult male was collected on Sinkut Mountain, September 28, 1952. The species was recorded earlier on the basis of two sight records in May, 1945.

Sialia currucoides (Bechstein). Mountain Bluebird.—Locally scarce in 1945 and 1946, abundant during the autumn migration of 1951 (September 20-23) and relatively common as a summer visitant in 1952.

On June 27, 1952, a female was watched feeding four young on lepidopterous larvae which she gathered in a nearby clump of willows. It was a cold day with rain and wind and the young huddled together in a row on a bench by my cabin door. It was observed that they were fed in rotation and that not once did the female hesitate in choosing the one next in turn.

Lanius excubitor Linnaeus. Northern Shrike.—An adult, shot at Nulki Lake, December 30, 1947, and sent to me in the flesh, and an immature male taken near the same place September 27, 1952, are the first specimen records for the region. The subspecies is *L. c. invictus* Bishop.

Dendroica coronata (Linnaeus). Myrtle Warbler.—Previously identified in spring only and not supported by specimen representation, it has since been recorded in autumn. On September 21, 1951, a small number accompanying Audubon warblers flushed from the edge of a sedge meadow and were observed also in nearby lodgepole pines. Specimens collected on this date, and on September 26, 28, 1952, are young in first-winter plumage.

Xanthocephalus xanthocephalus (Bonaparte). Yellow-headed Blackbird.—In July, 1952, a colony of 10 pairs was established on nesting territories at Manson's Slough where none had nested in 1945—in that year approximately six pairs of red-wing blackbirds occu-

pied this marsh. As seems usual when yellow-headed blackbirds invade nesting grounds of the less aggressive red-wing blackbirds it is at the expense of the latter. Thus in 1952 the red-wing blackbird population consisted of only two pairs.

Loxia leucoptera Gmelin. White-winged Crossbill.—In 1951 an exceptionally heavy crop of spruce seed was produced; the crowns of some trees were so thickly hung with cones that most of the foliage was hidden and at a distance the trees seemed distinctly bi-color, russet above, green below. The abundance of food thus provided attracted numbers of white-winged crossbills that usually were accompanied by larger numbers of pine siskins. Specimens of the first were collected.

White-winged crossbills were plentiful at other places in northern British Columbia that year and that some, if not all, had nested late was indicated by the presence in the flocks of juveniles in first-plumage which had bills straight or nearly so. The species was not seen in 1952.

Junco hyemalis (Linnaeus). Slate-coloured Junco.—One male and one female in first-winter plumage collected at Nulki Lake, September 28, September 30, 1952, respectively, are identified as the subspecies *J. h. cismontanus* Dwight. The common junco of the region is *Junco oreganus montanus* Ridgway.

Zonotrichia coronata (Pallas). Golden-crowned Sparrow.—An immature female taken at Nulki Lake, September 29, 1951, represents a second record for the species, the first being taken in spring, May 6, 1945. Three other immature birds were observed in the Sinkut meadows, September 20, 1952.

Calcarius lapponicus (Linnaeus). Lapland Longspur.—At Nulki Lake, September 29, 30, 1951, a flock of 100± frequented a hay field in which were bare patches of sandy soil mixed with gravel. When flushed they circled the field in a compact flock restlessly moving from place to place and alighting for only a few minutes before taking flight again. Six inches of snow had fallen on September 24 and the temperature dropped to $10°$ Fah. in the night. As this storm was general it might account for the appearance of this species at a date so early in the autumn. Three specimens collected constitute a new record for the Vanderhoof region. The subspecies is *C. l. alacensis* Ridgway.

MAMMALS*

In 1951 and 1952 the results obtained from trapping small mammals at Nulki Lake were conspicuously different from those obtained in 1945 and 1946. Thus the shrews *Sorex cinereus* and *Sorex obscurus*, noted as very scarce in 1945, were abundant in 1952, while the reverse was true in respect of the population of *Peromyscus maniculatus*.

Trapping results were as follows: 1951, trapping period September 15-22, 60 specimens of six species in 360 trap-nights, viz.: *Sorex cinereus*—2, *Sorex obscurus*—1; *Peromyscus maniculatus*—6; *Synaptomys borealis*—3; *Clethrionomys gapperi*—11; *Microtus pennsylvanicus*—37. 1952, trapping period May 28-July 13, 188 specimens in 1330 trap-nights, viz.: *Sorex cinereus*—54, *Sorex obscurus*—15; *Microsorex hoyi*—4; *Eutamias amoenus*—2; *Peromyscus maniculatus*—25; *Clethrionomys gapperi*—10; *Microtus pennsylvanicus*—69; *Zapus hudsonicus*—2; *Zapus princeps*—7.

Sorex cinereus Kerr. Cinereus Shrew.—Scarce in 1951 and abundant in 1952, as has been noted. The 54 specimens were trapped in *Microtus* runways on the Sinkut meadows and on a sedge meadow on Sinkut Mountain, in willow swamps and in aspen woods.

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* Since this paper was prepared for publication two records of mammals not hitherto reported from the region have become available, viz.: *Lynx canadensis*, of which I have examined three specimens, and *Vulpes fulva*, recorded on the basis of a sight observation, by a reliable woodsman, during November, 1953.

Sorex obscurus Merriam. Dusky Shrew.—What has been said of the cinereus shrew was true, in somewhat less degree, of this species. One specimen was taken in 1945, another in 1951, and 15 in 1952. It occupied the same habitats as the smaller species.

Microsorex hoyi (Baird). Pigmy Shrew.—Four specimens of this rare shrew were collected in 1952 on the Sinkut meadows: two—June 4; one—June 8; one—June 11. The first was taken in a trap set beside a pile of aspen stumps on land cleared in 1950, the second in a *Microtus* runway under tall, dead grass. The habitat in which the third was taken comprised a tangle of shrubbery and logs, that of the fourth grass and forbs margining an aspen wood.

These represent a new record for the region. The subspecific status has not been determined.

Ursus americanus Pallas. Black Bear.—The black bear population has increased in numbers since 1945 and many have been shot by local residents. On Sinkut Mountain, September 28, I came suddenly on four together feeding on *Arctostaphylos* berries. One was a large animal, the other three were thought to be yearlings. All were black.

Ursus sp. Grizzly Bear.—In May, 1952, an adult grizzly bear, accompanied by a smaller animal thought to be a yearling, was observed several times by the forestry look-out officer on the summit of Sinkut Mountain. Later the tracks were identified by the local game warden but the animals were not seen again.

Mustela rixosa Bangs. Least Weasel.—In September, 1950, a house cat belonging to a Lakes District resident brought in a least weasel. When shown to me it had been partly eaten, but enough remained to identify it with certainty. This is the first authentic record for the region; several sight records by local residents can now be considered acceptable.

Glaucomys sabrinus Shaw. Flying Squirrel. Two specimens, collected at Nulki Lake in September, 1952, are identified as the subspecies *G. s. alpinus* Richardson.

Neotoma cinerea (Ord). Wood Rat.—One or more wood rats which had established winter quarters in a small log cabin on Sinkut Mountain in September, 1951, stored a large quantity of dried fungi, *Boletus* sp. A table held a bushel or more and a smaller amount was piled in a corner of the cabin. In addition was the usual rubbish which wood rats accumulate in disused cabins. Whether or not the fungi was stored for food was not clear. It is known that pine squirrels eat, and make caches, of this particular species.

Clethrionomys gapperi (Vigors). Red-backed Mole.—Trapping returns indicate a smaller population in 1952 than in 1951. At no time, however, has the species been noted as abundant and very likely it does not fluctuate in numbers to the same extent as do *Microtus pennsylvanicus* and the two species of *Sorex*.

Six adults and five young in 1951 and 10 adults or sub-adults in 1952 were the totals trapped. An adult female, June 28, 1952, contained four small embryos.

Microtus pennsylvanicus Ord. Meadow Vole.—Scarce in 1950 but becoming common the following year when 37 were taken in 360 trap-nights. Of these 12 were adults or subadults and 25 young of various ages, some of the larger specimens in breeding condition. Two adult females, September 30, were nursing young.

In 1952 no special effort was made to trap *Microtus* nevertheless 69 were taken in 1330 trap-nights. As approximately 70% of the catch comprised young it was concluded that the population was again approaching a maximum.

Variations in Winter Muskrat Habitats and Harvests

Maurice M. Alexander*

State University of New York, Syracuse

The muskrat habitats of the Montezuma National Wildlife Refuge have been described under two major divisions, the main pool and the storage pool (Alexander and Radway 1951). There is considerable difference between the two areas, partly due to previous biological associations and partly due to the different dates of flooding. Each of these two pool areas can be subdivided into distinct habitat types. It has been the practice of the Refuge manager to divide the marsh into trapping units and in most cases the dividing lines coincide with the change in habitats. Therefore, a comparison of trapping units is essentially a comparison of habitats. Although the marsh areas are not necessarily divided the same each year, the most common division and the one used during the 1948 trapping season is three units in the main pool area and two units in the storage pool area.

TRAPPING UNITS

Unit 1, 729 acres, is the northern part of the storage pool. The productive area of this unit is the Tyre marsh of 82 acres (fig. 1). It is surrounded by woods killed by flooding which separate it from the other marsh areas. The vegetation is largely cattail (*Typha* sp.) and sedges (*Scirpus* sp.). By 1949 the marsh had developed into a very good muskrat habitat. Although it was flooded at the same time as the remainder of the storage pool its development has been slower, due in part to its isolation. The muskrat population was very low at first but as the vegetation improved the muskrats established themselves in larger numbers. It was first trapped as a separate unit in 1947 and these first muskrats were smaller than those from the other units. Since then the population and the size of the individuals have gradually increased. The reason for this early size difference involves food conditions, sex ratios and age ratios. Productivity was high and therefore many young muskrats were taken by the trappers.

Unit 2, the southern portion of the storage pool, contains 457 acres, 184 acres of which are open pool and marsh land. It is separated from Unit 1 by the woods and from Unit 3 by highway N.Y. 414. Prior to flooding, this unit was largely marsh hay (*Spartina pectinata*) and the muskrat population was very small. The area was flooded a year later than the main pool and required more time to develop into a muskrat habitat of cattail. This resulted in about a two-year difference between Units 2 and 3 in the development of the habitat and the muskrat population. Cattails were spreading over the area in 1944, and muskrats were first harvested in 1945. These were small and in poor condition. The muskrats increased to a peak population in 1947 when it was considered the best producing area on the Refuge. They were then
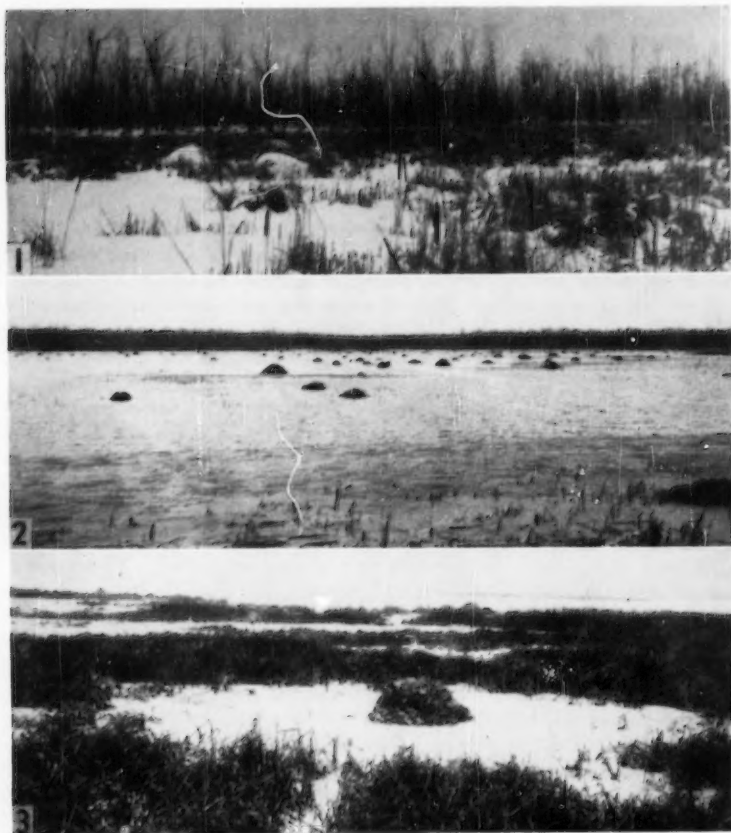
Figs. 1-3—1. Unit 1, Tyre Marsh, in the storage pool area; 2. Unit 2 in storage pool area showing general distribution of muskrat houses and the reduced vegetation; 3. Unit 3 in main pool showing a house and feeder in a bur-reed habitat.

equal in size and weight to those taken from the main pool. In 1948 the cattail areas became seriously depleted and this was the last year that houses could be found throughout the area (fig. 2). In 1949 the muskrats were confined to the cattail areas along the south and west sides of the unit.

Unit 3, the northern 366 acres of the main pool, is similar in many respects to Unit 4, which lies immediately to the south of it. The two are separated by a line connecting the northeast corner of the dike with the northwest end of Maple Island. This line passes through the Goose Pond region which is surrounded by bur-reed. Some of the original cattail growths occurred here. The western portion of the unit consisted of muck gardens that are now in cattail (*Typha glauca*), bur-reed (*Sparganium eurycarpum*), bulrush (*Scirpus fluviatilis*), and open water. Because the Goose Pond had marsh conditions around it and a basic population of muskrats, the unit developed quite rapidly and has remained a good producer of muskrats. The cattails have disappeared

from a large part of the unit but most of the *eaten out* areas are now revegetated with bur-reed. Variety is perhaps greater in this unit than elsewhere in the Refuge.

Unit 4, the middle and more eastern portion of the main pool, includes 727 acres between the line described above and another line separating it from Unit 5. This second line extends from the observation tower at the headquarters to the southern end of Maple Island. It includes that part of the original marsh located along the back channel and part of Goose Pond. These make up the existing deeper water areas. This unit underwent rapid development subsequent to the flooding as the cattails moved back into the shallower areas from the channels. It reached its peak production during the 1945 and 1946 seasons. After this the area of emergent vegetation became reduced and the muskrat population decreased accordingly. In 1948 it was composed largely of a narrow fringe of cattail along the western side and a mixture of bur-reed and cattail in the northern part adjacent to Unit 3. Since then a portion in the center of the open water area has been gradually returning to cattail.

Figs. 4, 5.—4. Unit 4 in main pool showing large open areas; 5. Unit 5 in main pool showing muskrat house in cattail habitat around Black Lake.

Unit 5, the southwestern part of the main pool consisting of about 480 acres, includes the dense cattail marshes west of the Refuge headquarters and around the Black Lakes. It is the largest of the original marsh areas and has remained about the best muskrat habitat on the Refuge. The vegetation is largely cattail, both the broad-leaf (*Typha latifolia*) and the blue flag (*T. glauca*). No serious *eat-outs* have occurred in this unit and the increased depth of water has not appreciably moved back the margin of the vegetation. The muskrats were always abundant in this unit and many of the extremely old and heavy individuals were taken here during the first few years of trapping. Now some of the smallest as well as the largest are taken here.

This discussion of the different units reveals that their numbering is in reverse order to their ecological development into good producing muskrat habitats. The lower the number of a unit, the more recent is its development.

TABLE 1.—Sex ratios by month and trapping unit for 1948

Month	Sex	Unit 1	Unit 2	Unit 3	Unit 4	Unit 5	Total	Per cent of season's catch
Jan.	♂	43.9	43.7	46.2	48.8	46.6	45.4	64.5
	♀	56.1	56.3	53.8	51.2	53.4	54.6	
Feb.	♂	42.6	48.0	50.0	51.5	50.9	47.3	24.2
	♀	57.4	52.0	50.0	48.5	49.1	52.7	
Mar.	♂	56.5	47.5	47.5	72.4	56.5	55.5	11.3
	♀	43.5	52.5	52.5	27.6	43.5	44.5	
Total	♂	45.9	44.9	47.2	51.1	48.8	47.0	100.0
	♀	54.1	55.1	52.8	48.9	51.2	53.0	
Per cent of season's catch		26.4	26.6	15.0	10.0	22.0	100.0	

1948 Harvest and Sampling Techniques

It was planned to harvest 5,000 muskrats (1,000 from each of the five trapping units) during the 1948 season. Severe winter conditions resulted in only 3,779 being taken. These were distributed as follows: 1,005 from Unit 1; 1,000 from Unit 2; 566 from Unit 3; 378 from Unit 4; and 830 from Unit 5. The sex and weight of each individual were recorded by Refuge personnel before the pelts were removed. An analysis of these recordings will be made in the following sections.

In order to obtain other information and to make detailed studies on the variations that occur between the different ages while in search for reliable aging characters, a sample was taken from the season's catch. Visits were made to the Refuge each week throughout the season. All of the day's catch was

utilized on each of these collecting trips. It was felt that this could be considered a fair random sample of the season's catch.

SEX RATIOS

A breakdown of the sex ratios for the 1948-season by month and unit is given in table 1. This shows that, in January, all of the units have similar sex ratios—about 45.4 per cent males. However, in February the proportion of males increased in all units except the Tyre marsh where it decreased slightly. The greatest variation of all occurred in March with some trappers still taking more females than males while others were taking largely males. For the entire season the units in the main pool produced proportionately more males than the storage pool units.

Fewer trappers were used in 1949 and these obtained their quota early in the season so that a similar breakdown would be of less value. However, the pattern was about the same and the main pool again produced a greater percentage of males than the storage pool.

TABLE 2.—Average weights in pounds and ounces of the 1948 catch by months and trapping units

Month	Sex	Unit 1	Unit 2	Unit 3	Unit 4	Unit 5	All units	Total
Jan.	♂	2—11.3	2—15.5	3— 0.2	3— 1.6	3— 2.4	2—15.7	2—14.0
	♀	2— 8.8	2—12.3	2—12.8	3— 0.2	2—14.9	2—12.6	
Feb.	♂	2—11.1	2—12.6	3— 1.5	2—13.9	3— 2.7	2—14.3	2—12.7
	♀	2— 8.4	2— 9.6	2—15.4	2—15.9	2—14.7	2—11.3	
Mar.	♂	2— 9.7	2—15.9	3— 0.4	2—11.9	3— 4.7	2—14.0	2—12.2
	♀	2— 6.2	2— 8.1	2—14.0	2—13.4	2—15.5	2—10.0	
All months	♂	2—10.8	2—14.8	3— 0.6	3— 0.3	3— 2.8	2—15.1	
	♀	2— 8.2	2—11.5	2—13.5	3— 0.1	2—14.9	2—12.1	
Total		2— 9.4	2—13.0	2—14.9	3— 0.2	3— 0.8	2—13.5	

It is interesting to note the variations between the sex ratios of the total catch for 1948 and those of the sample of muskrats taken periodically throughout the season. The outstanding feature is that although all of the muskrats taken on certain days were used in the sample, these were largely made up of days having a majority of males in the catch. The males made up 55.8 per cent of the sample and only 47.0 per cent of the catch. Although 60 per cent of the days in the season had more females than males only 27 per cent of the sampling days fell on such days of female majority. Inasmuch as the sex ratio of the sample is not representative of the season, the total catch sex ratios have been used instead of the sample.

WEIGHTS

The weights of the 1948 catch are shown in detail in table 2. The numbered units are in reverse order of their stages in habitat development; Unit

5 being the original good habitat around Black Lake and Unit 1, the Tyre marsh, now nearing optimum conditions. For the year 1948 there is a definite gradual increase in average weight from 2 lbs. 9.4 oz. for Unit 1 to 3 lbs. 0.8 oz. for Unit 5. Unit 1 was somewhat improved in 1949 so that its average weight increased while the others remained stable.

Age and weights were recorded for 541 of the sample of 552 muskrats collected in 1948. The young of the year averaged 2 lbs. 10.8 oz. and the adults 3 lbs. 5.4 oz. The average weight for all was 2 lbs. 13.7 oz., which is only 0.2 oz. more than the average weight of the entire harvest. This would indicate that it was a good sample at least as far as weight is concerned. The males were slightly heavier than the females, the adults 10.6 oz. heavier than the subadults, and the units produce an average heavier muskrat as the age of the habitat increases.

TABLE 3.—Average condylo-basal length in mm from 457 muskrat skulls taken during the 1948 trapping season

Unit	Sex	Subadult	Adult	Total
1	♂	63.4	68.1	64.0
	♀	62.9	67.0	
2	♂	63.6	68.3	64.3
	♀	63.4	68.3	
3	♂	63.4	67.3	64.5
	♀	64.0	68.0	
4	♂	63.4	67.3	64.9
	♀	61.9	67.2	
5	♂	64.5	68.4	66.0
	♀	63.9	68.3	
All units	♂	63.6	68.0	64.7
	♀	63.4	67.8	
Total		63.5	67.9	
Range		56.2-68.8	63.6-76.2	

BODY MEASUREMENTS

Body measurements are available for only the sample taken during the 1948-season. Inasmuch as it would be desirable to correlate these measurements with age, those that were of undetermined age are omitted, leaving 541 for the basis of these calculations. However, a few recordings cannot be used for each of the measurements due to such things as broken tails, and lost feet.

Four measurements will be considered, and the discussion of them will be centered about the tables showing average measurements for each sex, age, and trapping unit.

Body measurements are of little value in the determination of age (Alexan-

TABLE 4.—Average zygomatic breadth in mm from 454 muskrat skulls taken
during the 1948 trapping season

Unit	Sex	Subadult	Adult	Total
1	♂	38.3	41.7	38.9
	♀	38.3	40.7	
2	♂	38.5	42.4	39.2
	♀	38.6	42.3	
3	♂	39.0	41.9	39.9
	♀	39.4	42.3	
4	♂	39.0	42.3	40.3
	♀	38.6	42.1	
5	♂	39.0	42.6	40.4
	♀	38.9	42.1	
All units	♂	38.7	42.3	39.6
	♀	38.7	41.9	
Total		38.7	42.1	
Range		34.8-42.0	38.2-47.2	

der 1951). This is due largely to the great variation that occurs between
individuals of any age; the range of the measurements for subadults being
very near the range of measurements for the adults. However, these measure-
ments are of value when considered in terms of total populations instead of
individuals. In such cases the arithmetical mean represents the populations
fairly well.

The total length averages (including tail) are based on 533 muskrats.
Although variations in the averages are not very extensive, a few definite fea-
tures can be noted. The adults average 24.2 inches in length while the sub-
adults average 22.4 inches, a difference of 1.8 inches. The males were equal
to or slightly longer than the females for each age and trapping unit but this
difference is very small, the males averaging 24.2 inches and the females 24.1
inches. A gradual increase in average length can be seen with the develop-
ment of the habitat from 22.2 inches in Unit 1 to 23.5 inches in Unit 5. The
final average of all 533 muskrats is 22.9 inches in length.

The length and width of the tails also were recorded for 533 individuals.
The average tail length for the subadults was 9.3 inches and for the adults
10.0 inches, a difference of 0.7 inch. The tail widths were only one six-
teenth inch different, the subadults averaging 13/16 and the adults 14/16
inch. The two sexes were the same for both tail length and width as were the
trapping units except the one representing the youngest habitat, which aver-
aged 1/16 inch less in width and about 0.4 inch less in length. Casual obser-
vations from handling the muskrats in the field indicated that the widths of
tails differed in the various units. However, these data indicate that this is

not the case. In the years when Black Lake produced much larger muskrats than the storage pool this difference in tail width could have been true.

The length of the hind foot has been considered by some as a possible indicator of age. Measurements taken on 538 muskrats show that the males average the same as the females, the subadults the same as the adults, and all units were the same, an average of 3.3 inches.

The summary of the body measurements shows that there is very little difference between the muskrats taken from the different units except Unit 1 (the Tyre marsh) which produces a slightly smaller average individual, partially due to a greater percentage of young muskrats. This probably would not be noticeable in the field. The adults are somewhat longer than the subadults but have the same size feet. The males are the same size as the females except for a slight increase in total length.

SKULL MEASUREMENTS

Many measurements could have been taken on the skulls of the individuals in the sample, but the nature of the study did not justify the collection of these additional data. However, measurements were taken indicating the maximum size of the skull including the total or condylo-basal length and the total or zygomatic breadth. These two values for each skull make up the basis for the accompanying tables. The weight of the cranium (the skull without the mandibles) also was obtained. The frequence of broken skulls reduced somewhat the size of the sample.

The average condylo-basal length for each age, sex, and trapping unit is presented in table 3. There appears to be very little difference between the sexes but the usual gradual increase from the most recent developed muskrat habitat to the oldest again is evident. The difference between the adults and subadults is considerable and, depending upon variations that might occur within each age, this measurement could possibly be used as an indicator of age.

Similar data for the zygomatic breadth of the skull are given in table 4. Again there appears to be very little difference between the males and the females. The variation between the trapping units also is similar—the size increasing gradually with the increase in age of the habitat. The difference between the two ages is quite marked and therefore this measurement can be used as an indicator of age (Alexander 1951). The average size of the subadults (38.7 mm) and the average size of the adult (42.1 mm) have a difference of 3.4 mm.

The data gathered on the cranium weights of 425 individuals show the same relationship. There appears to be a small difference in the sexes, 0.5

TABLE 5.—Ages of 541 muskrats taken during the 1948 trapping season by trapping units

| Unit | Subadult | | Adult | |
	Number	Per cent	Number	Per cent
1	119	79.9	30	20.1
2	107	82.3	23	17.7
3	61	77.2	18	22.8
4	41	57.7	30	43.3
5	64	57.1	48	42.9
Total	392	72.5	149	27.5

TABLE 6.—Ages of 541 muskrats taken during the 1948 trapping season by month

Month	Subadult		Adult	
	Number	Per cent	Number	Per cent
Jan.	246	73.4	89	26.6
Feb.	93	71.5	37	28.5
Mar.	53	69.7	23	30.3
Total	392	72.5	149	27.5

gram; considerable difference in the ages, 3.1 grams; and a gradual increase with the age of the habitat, 10.1 grams in Unit 1 to 11.3 grams in Unit 5, an over-all average of 10.5 grams.

FAT DEPOSITION

At the time of the anatomical study of the sample taken in 1948, the visceral fat from the muskrats on certain scattered dates was weighed. This included the fat in three general locations: (2) below the stomach and along the pancreas, (2) in the region of the kidneys, and (3) along the reproductive tract. Although there remained small areas of fat not included, it is believed that this measurement should represent the condition of the muskrat and show trends in fat deposition. Fat located in the superficial fascia could not be weighed inasmuch as a variable portion of it remained on the pelt when removed by the trapper.

The weights of the fat taken from 296 muskrats were studied. The males (21.4 grams) consistently had more fat than the females (14.3 grams), and the adults (18.1 grams) usually had more fat than the subadults (13.0 grams). The area with the smallest and lightest muskrats also produced the least amount of fat (10.8 grams in Unit 1) while the area of largest and heaviest muskrats had the greatest fat production (18.4 grams in Unit 5). This is to be expected if the condition of the habitat has influenced the growth and development of its inhabitants. As might be expected, the amount of fat increases from an average of 13.2 grams in January to 17.3 grams in February followed by a decrease in March to 14.4 as the breeding season is approached.

AGE CLASSES

The variation in age classes on the five units is shown in table 5. It is of interest to note that the younger areas, Units 1 and 2, which produce slightly smaller muskrats than the older areas, have a greater per cent of subadults. It is only reasonable to expect that on newer areas the productivity would be higher. The ratio of adults to subadults is an indication of that productivity. Where subadults exist in above normal quantities, there must be a reduced average weight and size for the total catch.

There appears to be a definite trend for the changes in age classes throughout the season (table 6), the adults increasing from 26.6 per cent in January to 30.3 per cent in March. However, the effect that this would have on their average weight as the trapping season progressed is partly offset by the change in sex ratio with age. The slightly heavier males make up 55.7 per cent of the subadults and 53.0 per cent of the adults.

TABLE 7.—Summary of averages for each unit to show relationship of the muskrat population to habitat advancement

Unit	% males	Weight lbs oz	Total length (inches)	Tail length (inches)	Tail width (inches)	Hind foot (inches)	Skull length (mm)	Skull width (mm)	Cranial weight (grams)	Visceral fat (grams)	% adults
1	45.9	2 9.4	22.2	9.2	13/16	3.3	64.0	38.9	10.1	10.8	20.1
2	44.9	2 13	22.8	9.5	14/16	3.3	64.3	39.2	10.2	15.1	17.7
3	47.2	2 14.9	23.2	9.7	14/16	3.3	64.5	39.9	10.6	14.2	22.8
4	51.1	3 0.2	23.2	9.6	14/16	3.3	64.9	40.3	10.9	15.0	43.3
5	48.8	3 0.8	23.5	9.6	14/16	3.3	66.0	40.4	11.3	18.4	42.9
Total	47.0	2 13.5	22.9	9.5	14/16	3.3	64.7	39.6	10.5	14.4	27.5

SUMMARY

The muskrat habitats of the Montezuma National Wildlife Refuge are described under five basic trapping units. The development of these units is explained and correlations are made between the muskrat weights and measurements and the habitats. Although there is considerable variation in the weights and measurements, there are definite trends in the average figures. From these data the following statements can be made.

As the season progressed the percentage of males and adults increased while the average weights decreased slightly or remained fairly stable.

The males weigh an average of 3 ounces more than the females, measure 0.1 inch longer and have a little more fat. Their tails are the same length and width and the hind foot the same length. The skulls of the males were slightly larger than the females.

The adults weigh an average of 10.6 ounces more than the subadults, measure 1.8 inches longer, have 0.7 inch longer and 1/16 inch wider tails, and have more fat. Their hind foot measurement averages the same. The adults also have a somewhat smaller percentage of males. The adult skull averages 4.4 mm longer and 3.4 mm wider than the subadult skull.

The older or more advanced the ecological development of the habitat toward optimum muskrat condition, the heavier and larger the muskrats produced. However the length of the hind foot was the same for all habitats. The older habitats produced a greater percentage of adults.

The relationships of these features of the muskrat population to their habitat can be seen better in table 7.

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Observations on Chipmunks and Mantled Squirrels in Northeastern California

Lloyd Tevis, Jr.

University of California, Davis

During an investigation into the influence of rodents on reforestation, the Division of Zoology of the University of California at Davis trapped, autopsied, and studied 1,340 chipmunks and mantled squirrels. This work was done in cooperation with the California Forest and Range Experiment Station of the United States Forest Service. Its aim was a better understanding of the biology of diurnal rodents which, primarily because of their seed-eating habits, are accused of hindering reforestation. This paper gives selected facts and conclusions which resulted from the survey. Food data were analyzed separately.

Trapping started in mid-September of 1950 and ended one year later. Chiefly it was restricted to the Quincy area, which includes mountainous, coniferous terrain within thirty miles of the town of Quincy in Plumas County of northeastern California. Four species of chipmunks (*Eutamias amoenus, speciosus, townsendii,* and *quadrimaculatus*) and the mantled squirrel (*Citellus lateralis*) constitute a population unit of the important diurnal rodents of the area at altitudes from 4,500 to 5,500 feet, but numerical ratios between them differ with habitat.

Distribution.—As a rule, each species of chipmunk occurs locally in association with environmental features common throughout most of its geographical range elsewhere (Johnson, 1943, presents distributional maps). In the Quincy area, however, the local distribution of rodents is complex. A reason is the merging of three distinctive and vast regions: the Volcanic Plateau to the north, the arid Great Basin to the east, and the towering granitic Sierra Nevada to the south and west.

In the following summary of local distribution, which was determined by trapping, the terms "Volcanic Plateau," "Great Basin," and "Sierra Nevada" apply to the Quincy area only and are intended to suggest a degree of environmental differences rather than a sharp separation.

E. amoenus. The one species that delights in open and arid forests of ponderosa pine. where sagebrush (*Artemisia tridentata*) and bitterbrush (*Purshia tridentata*) indicate predominance of Great Basin influences; it also thrives in mixed brushfields of whitethorn (*Ceanothus cordulatus*) and manzanita (*Arctostaphylos patula*) and in mixed coniferous forests of Volcanic Plateau, but not in similar brushfields and forests of Sierra Nevada.

E. speciosus. Common to coniferous forests and edges of brushfields of Volcanic Plateau both in the somewhat arid areas which approach the Great Basin and in the moister places suggestive of the Sierra Nevada; also in Sierran forests at higher elevations. It is not dependent upon lodgepole pine, as has been implied in the literature.

E. townsendii. Inhabits forests that are relatively dense, also brushy areas that are relatively moist of Volcanic Plateau and Sierra Nevada, but avoids arid forests of Great Basin. It is least often associated with the sun-loving mantled squirrel.

E. quadrimaculatus. The common species of brushfields and of open or partly open mixed coniferous forests of Sierra Nevada; not found in sagebrush-bitterbrush areas or coniferous forests of Great Basin; and of limited occurrence in Volcanic Plateau.

The northern limit of the range of the last-named species warrants consider-

ation. As drawn by Johnson (1943), it crosses Lake Almanor on the Volcanic Plateau. Trapping during a number of months confirmed the accuracy of this line. I found *quadrimaculatus* at the southwest but never at the northwest corner of the eight-mile-long lake even though the forest was continuous and, on the average, unchanged in composition and density.

To determine precisely where the range ended and whether gradually or abruptly, I maintained 180 traps for two days in September of 1951 at eighteen sites along a north-south line paralleling the shore a half mile inland. The results are given in table 1.

From the southwest corner to a point opposite the center of the lake, *quadrimaculatus* was abundant: its density not exceeded elsewhere in the Quincy area. Then abruptly as though coming against an invisible wall, the species ceased to exist.

To all appearances, trees, shrubs, forbs, ground litter, volcanic soil, lava rock, degree of slope, elevation, and food supply did not differ. Yet, a forest that supported *quadrimaculatus* at site 9, a half mile away was seemingly inimical to the species. Fatal competition with other kinds of chipmunks is not likely since I have many records of their being together.

This unsolved problem emphasizes the difficulty of understanding distributional limitation within the chipmunk group. But such an understanding is important, for if the requirements of each species were known, rodent control through manipulation of environment might be possible.

Hibernation.—Information regarding hibernation is useful for rodent control and for direct seeding operations to answer such questions as the following. For how long a period are seeds safe from hibernators? Does the weather

TABLE 1.—Numbers of mantled squirrels and chipmunks trapped near Lake Almanor, Plumas County, California, September 26-28, 1951. Site 18 is opposite the southwest corner of the lake, and site 1 opposite the northwest corner. Adjacent sites are approximately a half mile apart. Each had ten traps, which were inspected three times.

Site no.	C. lateralis	E. amoenus	E. speciosus	E. townsendii	E. quadrimaculatus
1	4	1	10	....	....
2	4	....	12	2	....
3	5	....	6	....	....
4	13	1	5	....	....
5	13	2	8	1	....
6	10	8	6	....	....
7	7	....	14	....	....
8	2	12	8	1	....
9	....	1	5	2	7
10	10	4	7	....	1
11	1	3	3	3	9
12	2	4	2	....	7
13	1	1	1	3	5
14	4	....	3	1	5
15	....	7	2	1	6
16	1	1	....	....	11
17	5	....	....	1	6
18	1	1	1	3	10
Total	83	46	93	18	67

affect the duration of that period? Does the rodent population disappear and reappear abruptly or gradually? Is there activity on warm winter days?

In 1950, adult mantled squirrels began to hibernate at the end of August or earlier, but most of the young of the year did not disappear until early October. The latest record for a healthy and active squirrel was October 22.

In contrast to this gradual withdrawal of the population, chipmunks, most of which did not start hibernating until the end of October, were scarce within two weeks, and the different species disappeared more or less simultaneously. The latest trapping record was November 29 (*E. amoenus* and *quadrimaculatus*).

Weather did not set the time when squirrels hibernated, for when they entered their winter's sleep it was hot and dry as it had been throughout the long summer. Chipmunks, however, were active until the first storm of the season, which, though bringing warm rain and followed by days of sunshine, induced a permanent chill in the forest. Individuals which delayed hibernating for two or three weeks became quiet, secretive, and relatively inactive.

The winter of 1950-51 was mild. Whenever snow fell, it was soon melted by rain. The ground was seldom frozen and numerous sunny days gave rodents every opportunity to appear. Throughout much of the winter I operated trap lines and hunted in favorable areas, but never trapped, saw, or heard a mantled squirrel or chipmunk. Even a food-producing garbage dump that swarmed with rodents the preceding fall was deserted.

Spring came earlier than usual. In Great Basin areas, filaree burst into flower, tree toads achieved full chorus, and red-tailed hawks courted a month before chipmunks and squirrels roused themselves. Therefore, I concluded that duration of hibernation at each locality is adjusted to average conditions and is not subject to vagaries of different years. A similar conclusion was indicated by Engels (1951) in studies on captives of the eastern chipmunk.

The date when rodents entered hibernation in the Quincy area varied little with locality, but locality profoundly affected the time of emergence. Animals at lower elevations and in Great Basin areas appeared earlier than those at higher elevations or at sites more typical of the Volcanic Plateau and the Sierra Nevada. For example, mantled squirrels and *E. amoenus* of the Great Basin began to emerge in mid-March, but at corresponding altitudes elsewhere they and the other species did not appear in significant numbers until mid-April. (I have one record of an *E. townsendii* on March 19 and one of an *E. quadrimaculatus* on March 25.)

Emergence of hibernators was a gradual process extending over a month. The first out were quiet and secretive, and then as the population swelled to a certain critical point, their behavior changed. They became bold, noisy, and aggressive; this gave the impression of a sudden explosion in numbers.

Hibernation fat.—It is known that hibernation fat accumulates in the bodies of mantled squirrels, but it has not been realized that the same is true of some kinds of chipmunks. Excepting for *E. amoenus*, of which few specimens were collected at the right time, I have records of hibernation fat in specimens of all species studied.

Fat develops subcutaneously, being especially thick in the inguinal region, and also appears in the coelom, where massive amounts cling to mesenteries

of the gonads and extend craniad on either side of the spine to engulf the kidneys. The average gain in weight for chipmunks is about twenty per cent. Because of the speed with which deposits develop and the subsequent rapid disappearance of animals into hibernation, the period when a fat chipmunk may be taken is short. On the other hand, since some adult mantled squirrels put on weight in early August while many young animals are unable to do so until October, there is an extended period when a fat squirrel may be taken.

A squirrel trapped in December had no fat. Apparently unable to hibernate, it was emaciated, weighed less than any other specimen caught that fall, and presumably would not have survived the winter.

On coming out of hibernation, more than half the chipmunks (excluding *E. amoenus*) and the squirrels have a remnant of fat, which is dirty-white, dull, and cheese-like in contrast to the pure white and glistening appearance of fresh deposits.

Reproduction.—In the Quincy area, mantled squirrels and chipmunks have one short annual breeding season, there is a single litter per female, and young animals reproduce in the breeding season following birth.

For study of breeding, accurate diagnosis of sexual status of killed specimens is essential. If a microscope is available, determination of fecundity in the male chipmunk and mantled squirrel is simple—when the cauda epididymis of a breeding animal is cut it exudes fluid teeming with spermatozoa. If a microscope is not available, gross appearance of sexual organs must be relied upon. (Mossman, Lawlah, and Bradley, 1932, give descriptions, terminology, and figures of the male reproductive tract.)

As is well known these organs enlarge tremendously from the quiescent state. Length of testis increases by two, width of cauda epididymis and prosstate by three, and length of seminal vesicle and diameter of bulbo-urethral gland by five.

Enlargement and post-breeding retrogression of testes are gradual, but size of seminal vesicles and bulbo-urethral glands changes abruptly. Therefore, as a rule, these latter organs are either small, which shows the animal is not breeding, or large, which indicates fecundity. The firm bulbo-urethral glands located on either side of the anus at the root of the tail can be palpated in the living animal. Table 2 gives approximate sizes of reproductive structures of fecund specimens.

Other indicators of male fecundity are the black scrotum and pendulous position of testes. Terms "scrotal" and "abdominal" used as criteria of fecundity are meaningless, for the small testes of non-breeding animals usually lodge in the scrotum as do large ones. Not then being pendulous, on superficial external examination they appear to be abdominal.

At the onset of estrus in the female, the genital eminence becomes turgid, the vulva perforate, and the uterine horns inflated and twisted. These features are not typical before puberty or after involution.

Nipples, which are not usually apparent until puberty, grow during estrus and pregnancy and reach maximum size at lactation. There is much individual variation, however, as some lactating females have smaller nipples than pregnant individuals. After lactation, the nipples decrease in size. They become

covered with scab-like skin which ultimately sloughs off, although sometimes not until pregnancy of the following year.

Mantled squirrels mate shortly after emerging from hibernation; chipmunks not until a month or so later. The breeding season comes earlier in Great Basin areas than at corresponding altitudes in the Volcanic Plateau and the Sierra Nevada. The period of mating by both squirrels and chipmunks lasts about four weeks. Most of my pregnancy records for squirrels and *E. amoenus* were obtained between April 27 and May 19; and for *E. quadrimaculatus* between May 27 and June 15. But there are many exceptions to the basic pattern.

Success of the 1951 breeding season is attested by the following embryo counts: *C. lateralis:* one specimen with 8 embryos; six, 7; fourteen, 6; eighteen, 5; three, 4; one, 3; average, 5.1. *E. amoenus:* four, 8; one, 7; five, 6; six, 5; one, 4; average, 6.1. *E. speciosus:* one, 5; two, 4; average, 4.3. *E. townsendii:* four, 5; one, 4; one, 3; average, 4.5. *E. quadrimaculatus:* two, 6; three, 5; three, 4; one, 3; one, 2; average, 4.4.

Five females of the sagebrush chipmunk (*E. minimus*) trapped near Vinton, Plumas County, at an altitude of 5,000 feet on April 13, 1951 were gravid. Two had 7 embryos; one, 6; one, 5; one, 4; average, 5.8.

Embryo absorption was rare. Among squirrels only five examples were detected, and among chipmunks, two. In this connection, embryo counts of squirrels in early pregnancy did not average larger than those of late pregnancy.

Except during the first two weeks after parturition, uterine scars were not reliable indicators of litter size. Corpora lutea often were not apparent unless the ovary was sectioned.

Young animals were well developed before being weaned and sent onto the forest floor to forage for themselves. The earliest date on which I recorded young squirrels was June 15, but at Lake Almanor they did not swarm until early July. Soon thereafter the automobile highway around the lake was spotted with crushed bodies.

Molt.—Mantled squirrels have one annual molt; its place on the physiological calendar depends on duration of the breeding season. In males it

TABLE 2.—Approximate size in millimeters of reproductive organs of fecund male chipmunks and mantled squirrels

	E. amoenus	E. speciosus	E. quadrimaculatus	E. townsendii	C. lateralis
Testis, length	11	15	16	17	20
Seminal vesicle, length	8	9	10	10	15
Bulbo-urethral gland, maximum diameter	6	8	8	9	9
Prostate, maximum diameter	4	5	5	6	9
Cauda epididymis, maximum thickness	3	3	4	4	6

comes when the sexual organs involute and in females usually after lactation. Accordingly, males molt earlier than females and with less individual variation.

Chipmunks are remarkable in having two molts: one to drab pelage of somber hue and another to bright pelage of gay color. The former occurs in September by all species, males and females, and by young animals and adults at approximately the same time. It is completed before hibernation begins.

The molt to bright pelage starts after termination of reproductive responsibilities: when sexual organs of the male involute and the female weans her young. Some males therefore sport a gay garb for two or three months, whereas many a female no sooner attains bright pelage, then she has to replace it with a replica of her old dull dress.

In general, drab pelage is worn for the reproductive period when animals tend to be secretive, and bright pelage at harvest time when they are bold and reckless.

Young squirrels and chipmunks molt after they begin to forage for themselves. The sparse, dull coat of immaturity is then replaced by a pelage indistinguishable from that of adults. Young squirrels keep this dress, until a year later, but the young of chipmunks ,soon undergo 'a second molt to drab pelage.

Sex ratio.—The sex ratio revealed by trapping varied too much from day to day and from place to place to justify conclusions. Sometimes there was a preponderance of males in the traps; at other times of females. During pregnancy and lactation, which should encourage wariness, females were often caught more readily than males. One observation, though, may be significant. While *E. amoenus* was emerging from hibernation between mid-March and late April, I trapped ninety-three males and only thirty-six females. Later the sexes were caught in approximately equal proportions.

Age. classes.—Success or failure of breeding season, downward or upward trend in numbers, and efficacy of control measures can often be judged by ratio of young animals to old. Accordingly, criteria are needed to distinguish between adults (animals more than a year old) and subadults (animals less than a year old).

Reproductive. organs. At the end of the breeding season, appearance of the reproductive organs distinguishes adults from subadults. The testes of adults are flaccid and somewhat bluish and have undulating or wrinkled blood vessels; those of subadults are firm, pinkish or whitish, with straight vessels, and average smaller. The uterine horns of adult females are long and thick; those of subadults are relatively short, thin, delicate, and thread-like. Nipples are present on adult females but absent or of pinhead size on subadults.

In the spring when the reproductive tract undergoes development in anticipation of breeding, appearance of sexual organs can not be used to separate age classes.

Skull characters. Adult squirrels have well developed sagittal crests and adult chipmunks lambdoidal crests, while subadults of the fall do not. Also, molariform teeth of adults are conspicuously worn in contrast to the deep valleys and sharp ridges on the teeth of young animals in their first autumn. From inspection of 779 skulls collected throughout the year, I concluded that

skull characters which distinguish adults from subadults during the fall are
not valid thereafter.   Individual variation is too great.

Body weights.   Mammals are sometimes aged on basis of body weight,
which, however, is affected by amount of food in the alimentary tract.   Intesti-
nal amounts vary within narrow limits.   But the quantity in caeca and stomachs
of squirrels and in stomachs of chipmunks fluctuates widely.   This was proved
by weighing caeca and stomachs (including contained food) of 287 squirrels
and stomachs of 748 chipmunks and, in each case, calculating the percentage
represented of gross body weight.

In squirrels the range was from 3% when stomach and caecum was nearly
empty to 29% when distended with a large quantity of food; the average was
13%.   The heaviest stomach weighed 54 grams or 21% of body weight.   In
chipmunks the range was from 1% to 22%.   Averages were between 6% and
8%.   Plotting calculations for each species on graph paper gave curves that
were skewed towards the lower numbers.

Therefore, I concluded that body weight is not a reliable criterion of age
unless amount of food in the alimentary tract is subtracted, and even then,
although adults average heavier than subadults there is overlapping between
classes, as shown by study of weights during the fall.   Evans (1949) observed
voles which increased at least twenty per cent in body weight within five min-
utes through water consumption.

Health and fleas.—Except for two emaciated squirrels, all specimens were
healthy, and fleas were not unusually abundant.

The numbers of hosts inspected and kinds of fleas found are given in table
3.   Of the two squirrel fleas, *Diamanus montanus* was relatively more numer-
ous in spring, and *Oropsylla idahoensis* in summer and fall.

Within the Quincy area, local distribution of chipmunk fleas of the genus
Monopsyllus was determined by type of terrain, not by species of chipmunk.

TABLE 3.—Fleas from mantled squirrels and chipmunks

	C. later-alis	E. amoe-nus	E. speci-osus	E. town-sendii	E. quadri-maculatus
Number specimens examined for fleas	267	174	111	37	122
Percentage infested	70%	57%	50%	65%	56%
Average number per infested specimen	4.4	2.2	1.9	2.8	2.4
Diamanus montanus	379	6	5	1	1
Oropsylla idahoensis	406	1	6	1	1
Monopsyllus eumolpi	18	193	33	17	35
Monopsyllus ciliatus	7	27	59	48	125
Catallagia sculleni	11	2	1	....	2
Malareus telchinum	1	1	....	....	....

M. eumolpi was commoner in relatively open and arid forests, and *M. ciliatus* in moist and closed ones. The former was abundant in Great Basin areas, the latter where Sierra Nevada influences predominated. Hence, *E. amoenus* was usually infested with *M. eumolpi,* and *E. quadrimaculatus* with *M. ciliatus.* But an *E. amoenus* living in a deeply wooded habitat commonly had *M. ciliatus;* and an *E. quadrimaculatus* occupying an open and somewhat arid habitat was likely to be infested with *M. eumolpi.* The same situation prevailed for *E. speciosus* and *E. townsendii.*

Hubbard (1947), who has trapped *E. amoenus* over most of its geographic range, stated that the farther east chipmunks were taken the more *M. eumolpi* and the fewer *M. ciliatus* were noted, until in the Great Basin regions the latter entirely disappeared.

Lice and mites were numerous on a few specimens, ticks and intestinal worms were scarce, and, surprisingly, no cuterebra were found.

Numbers.—Numbers of white-footed mice of the genus *Peromyscus* reached a low in 1951. Jameson (1952) studied their decline and attributed it to scarcity of mast and consequent failure of autumn breeding. If numbers of squirrels and chipmunks were likewise affected, direct seeding for reforestation at such a time might succeed, when depredation by rodents would be minimized. But as I indicated in an earlier paper (Tevis, 1952), squirrels and chipmunks did not suffer from lack of nutritious food. Eating the abundant hypogeous fungi, they became fat.

Few died while hibernating, for large numbers reappeared in the spring. For example, on May 7 at Lake Almanor, 109 traps set twenty feet apart, in seven hours caught 35 mantled squirrels, 11 *E. amoenus,* and 50 *E. speciosus,* a total of 96 animals.

From then until the middle of summer the numbers of rodents declined rather rapidly. But when young of the year joined the population at the climax of a successful breeding season, there was an impressive upsurge, the density soon equalling that of the preceding autumn. At Lake Almanor in mid-September of 1951, 180 traps inspected thrice in forty-eight hours caught 307 squirrels and chipmunks (table 1). The tremendous population represented by this figure would have been a serious threat to direct seeding operations.

I am indebted to Drs. Milton Hildebrand, E. W. Jameson, Jr., and Tracy I. Storer for advice and assistance.

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Natural History of the Vampire Bats of Eastern Mexico

Walter W. Dalquest

Midwestern University, Wichita Falls, Texas

Vampire bats of two species range throughout eastern Mexico from the southern limits of the republic northward to approximately 175 miles from the United States boundary. The common vampire, *Desmodus rotundus murinus* Wagner, is a common to abundant bat almost wherever it is found. The hairy-legged vampire, *Diphylla ecaudata centralis* Thomas, is one of the rarer North American bats but seems to reach its maximum abundance in eastern Mexico.

These disgusting but nevertheless interesting mammals do great damage to livestock and attack human beings on occasions. Domestic animals are weakened and sometimes die from loss of blood from the wounds inflicted by vampires, while the open wounds are a common site of infection by bacteria and parasitic insect larvae such as screw worms. Vampires are potential vectors of disease also. They are known to transmit rabies and some cattle diseases in Panama, Trinidad, and South America, and such communicable diseases as the hoof-and-mouth disease might easily be spread by vampires. In the British West Indies an intensive campaign has been carried out in an effort to rid the island of Trinidad of these dangerous animals. The writer is convinced that a similar campaign must soon be undertaken in Mexico. The following report, which may assist in such a campaign, is based on several years of field work in eastern Mexico, during which period approximately ten thousand vampires were examined.

In the uninhabited jungles of extreme southern Veracruz I found no vampires, although conditions, except for the absence of domestic animals, seemed to be ideal for these bats. Along the Rio Coatzacoalcos, at the northern edge of the uninhabited area, where people, horses, cattle and burros are again found, vampires again were encountered. Large game animals are abundant in the uninhabited area, but none of the many specimens taken showed evidence of vampire predation.

Probably vampires were rare to uncommon in eastern Mexico in prehistoric times, but the arrival of domestic animals accompanying the conquest of the country by Europeans presented the existing vampires with a constantly increasing food supply in the relatively helpless burros, horses, and cattle. The common vampire breeds throughout the year, is extremely shy, is probably safe from most predators in the caves it inhabits, is remarkably hardy, and has now increased in numbers until it is one of the commonest and most widespread mammals in eastern Mexico. It is adaptable enough to live in hollow trees and the structures of man and to live on the arid deserts as well as in the tropics. It is principally, perhaps almost entirely, dependent on domestic animals for food at the present time and may even attack man.

Recognition of vampire bats.—Vampires are large bats, measuring two to three inches from the tip of the nose to the rump. The forearm bone of the wing measures two to two and one-half inches. Vampires lack external tails

but there is a narrow, tail-like strip of membrane, the uropatagium, along the posterior edges of the legs and rump. The teeth of vampires differ from those of all other North American bats in that the anterior ends of the jaws possess large, flat, scoop-like canines and incisors that are in contact anteriorly, and the cutting edges of the anterior teeth in each jaw form a "V." The jaws of other bats contain large, pointed, canine teeth which are round in cross section and are never in contact; and usually there are several small, peglike, incisors separating the canines. Vampires have no noseleafs but do have naked pads at the ends of their truncated snouts which contain distinct, "U-shaped" grooves. The ears of both species are small and do not extend past the nose when laid forward. Vampires are of uniform body color.

The common vampire differs from the hairy-legged vampire in being larger, having shorter, coarser fur and in being reddish brown or rusty in color rather than dusky gray. The most prominent difference between the two species is found in the thumb. The thumb of the common vampire is more than one-half of an inch long and has a distinct, fleshy pad on the ventral side, midway between the base of the thumb and the base of the claw. The thumb of the hairy-legged vampire is only about a quarter inch in length and lacks the median pad. The hairy-legged vampire gets its name from the fur that fringes the uropatagium, along the inner sides of the legs. The uropatagium of the common vampire is almost naked.

Several species of fruit-eating bats, especially of the genus *Artibeus*, resemble vampires in size and also lack tails. In addition to possessing facial stripes and teeth of a different type, all fruit bats that might be mistaken for vampires have prominent, erect, noseleafs. Because fruit-eating bats so often occur with vampires, and are so often mistaken for them, it should be stressed that *any bat with a noseleaf is not a vampire!*

Handling live vampires.—Live vampires should be handled with extreme care, for they move swiftly and bite viciously, leaving wounds that are large and painful and which heal slowly, even when disinfected immediately. Heavy gloves would probably protect the hands but are clumsy to work with. After some painful experimentation the following method of handling the bats was developed. The bat is pinned flat with a quick slap of the palm, care being taken not to cover its head. The bats have such short necks that they can not turn their heads upwards or to the sides at right angles. Keeping the bat pressed down, a large flap of skin at the base of the neck, between the anterior edges of the wings, is pinched tightly between thumb and forefinger. A bat so held is completely helpless and can be examined or moved as desired. Vampires seized around the neck are unable to bite but can scratch unpleasantly and flap their wings.

Most mammal collectors kill live bats by placing their index finger against a bat's back, thumb on its chest, and asphixiating the animal by squeezing. This method is not recommended for vampires. They are so tenacious of life that they can survive several minutes of hard squeezing, time enough to exhaust the muscles of the fingers; and apparently dead animals that had been so treated often recovered. Fruit-eating bats of equal size or larger were quickly killed by pressures that seemed to have little effect on vampires.

Vampires display similar toughness when shot. A charge of shot sufficient to kill large fruit bats almost instantly did not kill vampires unless they were

actually struck in the hearts or heads. A shot into a cluster of fruit-eating bats usually brought down numerous dead and dying bats, and few wounded bats were strong enough even to try to escape. A similar shot into a cluster of vampires usually brought down more wounded than dead bats and, unless they were seriously wounded or dead, the vampires flew or scampered off along the ground. On some occasions a shot into a dense cluster of vampires would bring down a dozen or more individuals but every animal would hop, scurry, or fly away and escape.

Distribution.—Vampire bats range from South America northward through Central America and Mexico. The northernmost record of occurrence in eastern Mexico is in the coastal lowlands near Victoria, Tamaulipas (Baker, 1951). This locality is only 175 miles from the United States boundary. The northernmost record on the Mexican Plateau is near Presa de Guadalupe, in the state of San Luis Potosi. Doubtless the bats range even farther north.

Within their range in eastern Mexico vampires are among the most adaptable of mammals. They are found in the steaming jungles of the eastern side of the Isthmus of Tehuantepec, Veracruz; near sea level on the arid and coastal plain of eastern Veracruz; up to 6500 feet elevation in the mountains near Atotonilco el Grande, Hidalgo; in the brush and mesquit plains near Victoria, Tamaulipas; and far out on the cactus-and-yucca covered desert near Presa de Guadalupe, San Luis Potosi. Vampires seem to have occupied the range where they are now found for a long time, for Cushing (1945) reported the remains of a vampire from a fossil deposit in southern Nuevo Leon, associated with the bones of the sabertooth tiger and other Pleistocene mammals. This locality is near the northern limit of the range of the species at present and is also somewhat higher (7400 feet). Considering the length of time vampires have lived in eastern Mexico and their tolerance to elevation, climate, and varied habitat, it is most surprising that they do not range northward into the United States.

The number of vampires is regulated locally by the presence of suitable daytime retreats. The bats reach their greatest abundance in limestone areas, where there are numerous caves. They are adaptable animals, however, and in the absence of caves they are able to find substitutes in buildings, rock walls, or hollows of trees.

Feeding habits.—Food of vampire bats consists entirely of the blood of mammals and birds. The digestive tract, modified for a diet of blood, was first described by Huxley (1865) and more recently by other writers (see Parks and Hall, 1951). The vampire's method of feeding and the species of animals preyed upon vary in different parts of the country.

In the state of Veracruz the bats prefer to feed upon the blood of the burro, the little Mexican donkey, although horses are also extensively attacked. In areas where the bats are numerous it is a rare night that an unprotected burro or horse escapes being bitten. Two horses roaming near a cave containing a large colony of vampires near Potrero Viejo, Veracruz, were often attacked, became emaciated in about two weeks, and would doubtless have died, had they not been removed. Calves are commonly bitten, but adult cattle are bothered less by the bats, although some Brahma oxen weighing fully a ton

were observed with fresh vampire wounds on their cheeks. Vampires seem not to bite domestic fowls in Veracruz. The chickens and turkeys that belong to the country people usually roost, unprotected, in low trees and bushes near houses, and no report of vampires attacking these birds was ever received.

In the tropical, eastern part of San Luis Potosi also the vampires attack burros and horses, but they seem to feed upon the blood of cattle to a far greater extent than they do in Veracruz. Domestic fowls are a favored prey, and any chickens or turkeys that are not tightly penned at night are likely to be soon killed by the bats. On the Mexican Plateau of San Luis Potosi, the vampires seem to feed principally on horses and cattle. Burros are less common on the plateau but are heavily preyed upon where they do occur. Chickens are rarely molested on the plateau.

Relatively few sheep, goats, or pigs were examined for evidence of vampire predation. No direct evidence of molestation of these animals by vampires was ever secured, but the data are too slight to prove that they are not bitten. A number of large wild game animals, including deer, brocket, collared peccary, white-lipped peccary and tapir, were examined, but no scars that could certainly be attributed to bites of vampires were noted.

Many residents of Veracruz were asked whether vampires ever bit people, and all definitely denied that the bats ever bit human beings. Neither the writer nor any of his native assistants were ever attacked in several months of field work when the entire party slept in the open or in tents with open doors near known vampire colonies. The evidence of the natives becomes less conclusive, however, when one notes that the people of San Luis Potosi also vehemently denied that the bats bite human beings and were revulsed at the very thought. Children with unmistakable vampire bites were seen, but these bites, the people said, were bites of *brujas* or witches. Perhaps questioning the natives of Veracruz about witches would reveal that the vampires in that state bite people just as they do farther north.

Vampires do not leave their retreats until after darkness. Near San Andres Tuxtla, Veracruz, observations showed that the vampires did not leave their cave until several species of insectivorous and fruit-eating bats were on the wing. The vampires are rarely seen in flight, partly because they are extremely skillful at dodging out of the beam of a flashlight and partly because they fly close to the ground when they are hunting. Near Rio Verde, San Luis Potosi, Japanese silk "mist nets" were stretched between cypress trees near a vampire colony. No bats were taken in the nets until complete darkness. Once it had become dark, however, numerous vampires were trapped, and nearly all of them were taken in the lowest panel of the nets, less than one meter from the ground. The bats flew silently and were not heard until they had become entangled in the nets. This is in marked contrast to their noisy flight in the caves where they spend the day. More than 100 vampires were taken by chance in nets set at night in the open and in the jungle of San Luis Potosi. Most of the bats were entangled less than a meter from the ground. The bats were taken from the onset of darkness throughout the night, although most were taken about one hour after dark and relatively few were taken after midnight.

Vampires were observed on numerous occasions near the stables at Potrero Viejo, Veracruz, but were never seen in the actual act of feeding. The feeding

habits of captive vampires have been described by Ditmars and Greenhall (1935). Some vampires find their prey and fill their stomachs with blood in a short time. Near San Andres Tuxtla, Veracruz, vampires were taken as they were returning to their caves with freshly-filled stomachs about a half-hour after they had left for their evening hunt. Unlike insectivorous and fruit-eating bats, which commonly retire to rest after feeding in some sheltered place other than the place where they ordinarily spend the day, vampires seem to return to their daytime retreats after they have fed. No vampires were ever seen, nor were their unmistakable droppings ever noted, in places where they did not live by day. Perhaps the high-protein diet of the vampires makes it unnecessary for the bats to fill their stomachs more often than once a night, while the resting period of other bats is only a respite before hunting is resumed.

In eastern Mexico vampires usually bite burros, horses, and cattle on the cheeks and necks, at the bases of the ears, or slightly below. Oxen are usually bitten on the cheeks, and chickens and turkeys on the legs just above the place where the feathers begin. In South America it has been reported (Hensel, 1896; Caraccolo, 1895; Allen, 1916) that cattle are bitten above the hooves, chickens on the necks, and human beings on the fingers, toes or noses. In Mexico, human beings are usually bitten on the cheeks, over the zygoma, and rarely if ever on fingers, toes or noses. Strangely enough, children are bitten far more often than adults, and women more often than men. One might think that vampires are repelled by whiskers, although one alleged victim had a full beard.

Wounds made by vampires are unmistakable. A round or oval area of skin, three or four millimeters wide, five millimeters or more in length, and a millimeter or so in depth, is completely bitten away. The wounds bleed freely; even when disinfected and bandaged they sometimes bleed for a half-hour. Horses and burros bitten in the night are marked by long streaks and blobs of coagulated blood on the following morning, and blood-sucking insects usually make a swarm about the wound itself, while yellow-jacket wasps chew on and enlarge it.

Vampires bite with a swift outward thrust of the head, nip as the outward motion is completed, and quickly withdraw again. No attempt is ever made to hold or chew. The teeth of the vampire are razor-sharp. On one occasion when the writer was demonstrating the biting motion of the vampire with a cleaned skull, the teeth came into contact with the edge of his thumb. The teeth bit in effortlessly, and made a deep cut, which bled profusely and required bandaging.

Vampires probably spread diseases among the animals they attack in Mexico, as they do elsewhere (Clark and Dunn, 1932, 1933; Hurst and Pawan, 1932; Pawan, 1936), but this subject has been little investigated in Mexico. Considering the broad range of the vampires, their abundance, and the extent to which they feed on domestic animals, it is safe to say that no lethal disease is being transmitted by them at present or the Mexican livestock population would be decimated.

It should be noted, as suggested by Allen (1939) that vampires may not be efficient vectors of diseases in many cases. There is a possibility of infection when the bat bites its victim, but, if the blood runs freely, as it usually

does, the bat laps the blood running from the wound and does not further come into actual contact with the exposed flesh. If, however, the flow of blood is less copious, the bat actually licks the raw wound and infection is probable.

Daytime retreats.—Almost ninety percent of the more than 100 vampire retreats known to the writer are caves. Other retreats include deserted buildings, mine shafts, old wells, hollow trees, and crevices in stone walls. The number of vampires composing a colony varies from a half-dozen to well over 2000. Most colonies include about 100 bats.

Inhabited caves, where caves are numerous enough to allow the bats any choice, are large enough to have entrances sufficiently small that there are areas of almost complete darkness. Vampire caves are usually so dark that the bats cannot be seen without the aid of a flashlight. Even in such dark places, the bats hide at the apices of pits or crevices or behind ledges, where there is even less light. In areas where there are no dark caves, the bats creep into the deepest and darkest crevices that are available.

Caves inhabited by vampires were found in sandstone, gravel, basalt, conglomerate, earth, and especially limestone. The caves vary from shallow niches in cliffs to tunnels more than a mile in length, but in the latter case the bats were not found at the extreme end of the cave. Some caves had enormous entrances, more than 100 feet across; others would scarcely admit the body of a man. When choice of a number of caves is offered, however, vampires seem to prefer caves with small entrances and with dark rooms, twenty feet or more in diameter, near their mouths.

The presence of vampires in a cave can be detected as soon as the cave is entered, often before. The bats customarily group themselves in tight masses within their retreats and a deep pool of stinking liquid or semi-liquid feces, composed entirely of digested blood, collects under the roost. The decay of this "vampire pool" releases a large quantity of free ammonia which pervades the atmosphere of the cave and the area near its mouth. An invertebrate fauna is usually found in the mud at the edges of vampire pools, with larvae of insects and some isopods living in the muck itself. The pH of one vampire pool, tested with indicator paper, was 13.

When a man enters a vampire cave, and the bats are not alarmed, he rarely hears a sound, even from tightly packed clusters of 100 or more bats. Once frightened, however, the bats are noisy and flee by creeping swiftly away, using their feet and long thumbs, or by dashing off in headlong flight. Their flight makes a characteristic sound, a loud swishing, with the first wing beats loud and with the later beats diminishing in volume. An observer quickly learns to detect the flight noise of a vampire and identify it, even when bats of several other species are flying about in the cave. Vampires are rarely seen when they fly. They take off from concealed perches and fly in straight lines away from the observer, keeping in the shadow and avoiding flashlight beams. Other species of bats keep more in the open and wheel about when they fly. On some occasions an entire colony of vampires will have a deep crevice into which they retreat when disturbed. Near Potrero Viejo, Veracruz, a colony of about 100 bats flew immediately to a rock wall by a deep, narrow crevice into which they moved in single file through a small opening. Each bat patient-

ly waited its turn to enter, and shooting into the waiting bats caused only a few of them to fly.

The agility of vampires is surprising. They can creep along on a rock wall almost as fast as a man can walk on the level. Wounded bats that are unable to fly sometimes run along the ground, using their legs and wings, so fast that a man must run to catch them. On one occasion a vampire was seen to jump, using feet and thumbs and with wings closed, a distance of about twelve inches. Vampires resemble large spiders when they are moving about on the wall of a cave.

Unlike some other species of bats, vampires do not carry their young with them in flight. Retreats visited after the vampires had left on their hunting flight still contained bats too young to fly. When colonies are menaced, the adult vampires promptly desert the young, leaving them clinging to the retreat while the parents take shelter in crevices or distant parts of the cave.

When some vampire colonies were disturbed several times in a period of a week or so, the bats deserted the caves. In other instances colonies were investigated and specimens collected almost daily for two weeks or more, but the bats did not leave. In the latter cases it may be that no other suitable caves were available in the vicinity.

Some species of cave-inhabiting bats emerge from their caves in the hot, tropical midday and cling to shaded recesses near the mouths of their caves, ready to dart into the depths at the least alarm. This habit was noted only once among vampires. On the open desert near Presa de Guadalupe, San Luis Potosi, a cave was visited at midday and three common vampires flew into the cave from a perch near its mouth when the party drew near. In all other instances the bats remained deep in the caves throughout the day.

The ability of vampires to substitute the structures of man for their more natural retreats is shared by many other species of bats. A hundred or more abandoned native huts, constructed of bamboo or sticks and with thatched roofs, were examined for bats but vampires were never found in such well-lighted, warm and dry places. Abandoned stone or concrete buildings, on the other hand, were usually occupied by vampires if they were dark and cool.

Bats of other species are usually found in the caves and other retreats where vampires live, although no other species of bat was ever found in a cluster of vampires. Species associated with vampires in Veracruz and San Luis Potosi include: *Balantiopteryx plicata, Balantiopteryx io, Saccopteryx bilineata* (in a hollow tree), *Pteronotus davyi, Chilonycteris rubiginosa, Chilonycteris personata, Mormoops megalophylla, Micronycteris sylvestris, Mimon bennettii, Glossophaga soricina, Leptonycteris nivalis, Choeronycteris mexicana, Carollia perspicillata, Artibeus jamaicensis, Artibeus lituratus, Natalus mexicanus, Myotis nigricans,* and *Molossus nigricans* (in a hollow tree).

The habits of the hairy-legged vampire are less well known than those of the common vampire. Observations in Veracruz, Hidalgo, and San Luis Potosi indicate that this species is less colonial than the common vampire, does not live in tight clusters in the caves it inhabits, and consequently does not form a "vampire pool," and does not flee immediately to some pre-selected retreat when molested. All of the dozen or so retreats of this species discovered by the writer were caves except for an old mine tunnel in Hidalgo (Dalquest and Hall, 1947).

Young.—Both species of vampires bear but a single young. Young of the common vampire are born at all months of the year, and every colony of moderate size or larger that was examined contained young bats of various ages as well as pregnant females and adult, non-lactating females. The hairy-legged vampire seems to have a regular breeding season and may have but a single young a year. Females of this species group together when the young are born, though not in tight colonies like common vampires. Near Xilitla, San Luis Potosi, three females with very large embryos were taken on March 10, 1950, and about 35 bats of this species seen in the same cave on July 12, 1950, were mostly females with half-grown young.

Protection from, and control of, vampires.—Sanborn (1931) reported that in South America he was able to keep vampires from killing his horses by hanging lighted gasoline lanterns near the animals during the night. In San Luis Potosi domestic fowls are protected from vampires by placing them at night in pens of chicken wire or closely-woven bamboo.

Protection of range cattle and horses, however, seems hopeless at the present time. Unless cattle and horses could be completely enclosed at night the bats would get at them. Stables with openings as small as a few inches across failed to protect the horses in some places in Veracruz, and similar results were reported by Hurst and Pawan (1932). In most of eastern Mexico there are no stables or barns of any kind, nor can the country people afford to build them. Penning of the half-wild range cattle is utterly impossible.

Destruction of the vampires in their daytime retreats seems to be the most practical method of control, but a few experiments made by the writer indicate that this will be far from easy. Any control method must be cheap and simple. The shyness and toughness of the vampires has been mentioned; killing the bats by hand, whether with nets, guns, or clubs, will be largely ineffectual. In the few native attempts at control witnessed by the writer, harmless fruit-eating bats were killed in numbers while few vampires or none at all were destroyed.

Sealing up the caves in which the vampires are living offers some promise, when caves are small enough to seal and have one or a few entrances. This would be a laborious undertaking because the vampires can creep through even rather small crevices and effective sealing would require the use of very small stones. The writer attempted to close off the entrance to one cave with a heavy seine net. The cave mouth was well adapted for this, having relatively smooth, even walls about the mouth and some narrow crevices into which the net could be wedged. The cave was examined that night but, although friut-eating bats were still confined to the cave, the vampires had forced their way between the cliff face and the net and so escaped. Some of the vampires returned and re-entered the cave during the night, again forcing their way between the net and the face of the cliff. Only by sealing the net to the stone with some adhesive could the vampires have been trapped. Caves could doubtless be sealed off with cement but this would be a method of control far too expensive for most Mexican ranchers.

Smoking the bats out with wood smoke is also ineffective. When the writer wished to obtain specimens of vampires from a deep well on the coastal plain of Veracruz, a bucket filled with smouldering corn cobs was lowered into the well on a long rope and the rope shaken. The well filled with dense smoke in which the vampires could be heard flying from perch to perch but no bats

were driven out. An hour later, at the suggestion of a watching Mexican, the bucket was again lowered, filled this time with glowing corn cobs, green grass, and dry chili peppers. The well again filled with smoke and the vapor from this concoction was so acrid that even a trace made the watcher's eyes water and irritated the nose and throat. Two hours later the bats could still be heard flying when stones were dropped into the well. A native boy, lowered to the bottom of the shaft the next day, reported that there were no dead bats in the well. The bats deserted the well for a few days but were again living there a week later.

Fumigation of the vampire caves with poisonous gas is practical only in the case of small caves with a few entrances, and in any case would be too expensive and dangerous to appeal to most ranchers. Any control measure must be adapted for use by poor and uneducated people. The possibility that crude oil or creosote, painted on the necks and cheeks of horses and cattle, might protect them from vampires should be investigated. Vampires are so adapted to feeding on domestic animals at the present time that actual protection of livestock might result in wholesale starvation of the bats. In some large areas of eastern Mexico there is little else upon which they might feed.

In any event vampires are a menace to livestock and the health of man in eastern Mexico at the present time and may be expected to be increasingly so in the future. Control of the bats promises to be a problem of major importance, and effective control may be impossible.

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A Survey of Adaptive Relationships of Dentition to Diet in the North American Iguanidae*

Nicholas Hotton III**

University of Chicago, Chicago, Illinois

Dental morphology of poikilothermal tetrapods is frequently discussed in paleontological literature. It is important partly because many fossil forms are known chiefly from teeth and skull fragments, and partly because of the hypothesis that dental morphology is strongly influenced by selective factors operating through diet, and should therefore provide information regarding habits of the forms in question.

Direct evidence of the selective influence of diet upon dentition can be found, obviously, only among living forms. Of living poikilothermal tetrapods, lizards appear to be the best subjects for a study of diet and dentition, because of their relatively great diversity of dental structure and of diet, and also because of their ready availability. Dietary studies of lizards occur with moderate frequency in the literature, and are discussed in a subsequent section of the present paper. Studies of lizard dentition, on the other hand, are exceedingly rare, and most are concerned with fossil forms. Consideration of the relation of diet to dentition appears to be confined to one species, *Varanus niloticus*, which, however, has been discussed rather intensively (Lönnberg, 1903; Schmidt, 1919; Cowles, 1930); no comparable investigation of other lizards has yet been made.

The present study is an attempt to remedy this situation, by comparing diets and dentitions of several species of lizards. The chief aim of this comparison is to determine, in general, whether lizard dentition shows adaptive response to selective factors operating through diet, or whether its evolution is so intimately related to that of other characters not directly influenced by diet, that the effect of diet on dentition cannot be discerned. A corollary of this aim is to determine directions of any adaptive trends of lizard dentition, which may be interpreted as being due to selection through dietary factors.

All of the lizards chosen for investigation are North American members of the family Iguanidae. These forms are ideal subjects for four reasons. First, their comparatively well-understood taxonomy defines the North American iguanids (exclusive of *Anolis*) as a closely-related phylogenetic group; in general, morphological basis for this taxonomy rests upon other than dental characters. Closeness of phylogenetic relationship suggests that the genetic substrate of dentitional morphology is relatively homogeneous; the closer the relationship between lizards being compared, the more readily can dentitional differences between them be ascribed to different diets (if, of course, diets are different). The second reason for selecting the North American iguanids for study is that they exhibit a considerable variety of dentitions. The third reason is that members of the group are readily available in numbers, and the

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fourth is that adequate data concerning diet are almost entirely restricted to the North American Iguanidae.

Material upon which this study is based comes from two separate sources. Information concerning diet is drawn almost entirely from published accounts. Data concerning dentitions are derived from examination of series of preserved specimens from the collections of the Chicago Natural History Museum. Additional details concerning both diet and dentition have been obtained from a number of lizards collected by the writer, near Seymour, Texas, during the spring of 1950. Table 1 lists the species studied, and gives size of samples from which dietary and dentitional data are drawn.

Taxonomy

The taxonomy followed in the present paper is that proposed by Mittleman (1942) and Smith (1946). According to this scheme, all of the North American iguanids except *Anolis* are derived from the Central American genus *Ctenosaura*, or a closely related form. The phylogeny is dichotomous, one main line leading to *Sceloporus* and its derivatives, and the other to *Crotaphytus* and *Gambelia*; as Mittleman states, neither group can be considered older or more primitive than the other. *Uta* and *Urosaurus* are interpreted as direct but independent descendants of *Sceloporus*, and *Phrynosoma* is believed to be an early branch of the line that led to *Sceloporus*. *Holbrookia* and *Callisaurus* are part of a later branch of the pre-*Crotaphytus* line.

The only difference between the views of Mittleman and Smith is in the disposition of *Dipsosaurus* and *Sauromalus*. Mittleman considers them very early offshoots of the pre-*Crotaphytus* line, and Smith believes that they had appeared before differentiation of the ancestral stock into *Crotaphytus*- and *Sceloporus*-branches; this is a minor difference and is not pertinent to the

TABLE 1.—Species and numbers of references and specimens which furnished the basis for this study

Species	Diet Sample		Dentition Sample
	Number of accounts drawn from literature	Number of individuals	
Sceloporus g. graciosus	9	More than 2500	20
S. undulatus elongatus	3	105	20
S. magister	2	68	15
Uta s. stansburiana	6	More than 9000	21
Urosaurus ornatus levis	2	89	20
Crotaphytus c. collaris	2	104*	23
C. c. baileyi	5	166	21
Gambelia wislizenii	4	258	21
Holbrookia texana	0	32*	23
Callisaurus draconoides ventralis	3	70	20
Phrynosoma platyrhinos	see pp.	....	11
P. douglassii ornatissimum	see pp.	....	9
P. cornutum	0	23*	11
Dipsosaurus d. dorsalis	see pp.	....	15
Sauromalus obesus	see pp.	....	10
Ctenosaura similis	see pp.	....	15

* Includes specimens collected and examined by present writer.

present discussion. The question of whether or not *Uta* and *Urosaurus* are generically distinct, as long as it be agreed that they are closely related to *Sceloporus*, is also immaterial to the present problem, as is the validity of the genus *Gambelia*, as distinct from *Crotaphytus*. The present writer follows Mittleman in using the name *Urosaurus*, and Smith in using the name *Gambelia*, in order to be consistent with the above phylogenetic outline.

A taxonomic question that bears to some extent on the present study is that of distinction between *Urosaurus ornatus levis* and *U. o. wrighti*. According to Mittleman, *levis* is a relatively rare subspecies, restricted to a small area in north-central New Mexico, while *wrighti* is far more common and ranges over most of Utah and northern Arizona, and northwestern New Mexico, where its range impinges against that of *levis*. Smith and Mittleman agree that most of the forms discussed in the literature as *levis* actually pertain to *wrighti*, especially those collected in Utah and northern Arizona.

Data on dentitions of *Urosaurus*, as used in this study, are based upon specimens in collections in the Chicago Natural History Museum which are labelled *U. o. levis*, and the dietary data are based upon information in papers by Knowlton (1934, 1938), whose specimens are also assigned to *levis*. Specimens providing dentitional information are from Utah and northern Arizona, and those providing dietary information are from Utah. According to the conclusions of Smith and Mittleman, these specimens should be assigned to *wrightii*, but since they have been consistently labelled *levis* by competent taxonomists, the present writer prefers to call them by the latter name. Even though *levis* is perhaps incorrect as applied to these lizards, both dietary and dentitional data are based upon the same form, whether *levis* or *wrighti*, and the relations of both to other forms in the present series are probably essentially similar.

DENTITION

GENERAL CONSIDERATIONS

For convenience in description, the pleurodont iguanid tooth can be divided into two parts, root and crown. The root is the part by which the tooth is attached to the inner wall of the parapet formed by the premaxillary, maxillary, or dentary bone; it may be of considerably greater diameter than the crown. The crown projects beyond the margin of the parapet; it may be flattened laterally, and it shows greater or lesser development of accessory cusps, which when present are located anterior and posterior to the large main cusp. Teeth of many forms are constricted between root and crown; this constriction is called the neck, or shaft. In some genera, certain regions of the maxillary and dentary bones bear teeth that are higher than are those of neighboring regions; in others teeth are of essentially the same height all along the jaw. Teeth are replaced in a regular manner, in which alternate teeth in

the row are at approximately the same stage of development; replacement continues throughout life.

Occlusal relationships are such that the upper teeth are in a labial position with respect to the lower; the lingual edges of their crowns face the labial edges of the crowns of the lower teeth. The apices of the maxillary crowns lie between the dentary teeth when the jaws are closed. Normal occlusion probably does not bring crowns of upper and lower teeth into actual contact. Crown conditions that can be conclusively interpreted as being due to wear or abrasion are lacking, at least in specimens examined by the writer.

In this study, the term dentition refers to the maxillary tooth row. Premaxillary teeth are not considered in detail because in all genera under consideration, with exceptions noted, they are similar, being generally small, conical, and more or less sharp and recurved. The mandibular tooth row is essentially a mirror image of the maxillary row. The maxilla bears from about 15 to about 25 teeth in all forms studied, the most common number being from 18-20. This number varies only slightly from genus to genus, and is apparently closely related to the size of the individual with respect to the size of others of its species. Teeth are designated by number, starting with the most anterior maxillary tooth. Because of the possibility of loss, one cannot be sure that the first tooth in one individual is the same as that in another, so the procedure used here is to consider the teeth in groups of three, taking the height of the highest as indicative of the potential height of the other two. This method also tends to eliminate differences in height caused merely by teeth being at different stages of replacement. Since the question is not that of position and height of the highest tooth, but rather of the position of the region of highest teeth, and height of teeth in that region, the described procedure does not mask real differences.

Dentitions studied show tangible differences in the following characters: degree of development of accessory cusps of teeth; position of most anterior cuspate tooth; dental profile (differences in crown height in different regions of the jaw); slenderness of teeth; sharpness of teeth; and degree of lateral compression. In addition, a few dentitions are different from the rest in expansion of constriction of roots of teeth, and a few are different in placement of teeth in the maxilla.

DEFINITION OF DENTAL CHARACTERS, AND DESCRIPTION
OF VARIOUS DENTITIONS

For brevity, degree of development of accessory cusps is referred to simply as degree of cuspation in succeeding sections. It is defined by the following arbitrary stages:

Non-cuspate: Blunt, rounded, peglike crowns, or sharp, conical crowns.

Low degree: Crowns blunt but not rounded. Appear to have "shoulders" when viewed from labial aspect, but no clear groove separating main cusp from accessories.

Moderate degree: Crowns may or may not have clear-cut shoulders. Incipient grooves present on labial face, separating main cusp from accessories.

High degree: Crowns clearly shouldered. Grooves separating main cusps from accessories are clear-cut, but restricted to distal portion of labial face.

Very high degree: Accessory cusps form distinct entities in labial profile of crown, i.e., labial profiles of crown three-pronged instead of merely shouldered. Grooves on labial face well-developed, extending nearly to edge of maxilla in most cases.

These stages undoubtedly grade into each other, but each is distinct enough

for practical purposes; any attempt at finer distinction would exceed limits of accuracy. Table 2 presents the frequency of occurrence of each degree of cuspation in all samples of lizards studied. In table 2 and all subsequent tables, frequencies are given in terms of approximate percentages of the samples in which they occur.

In most of the lizards of the present series, degree of cuspation increases from anterior to posterior, the most anterior teeth being essentially non-cuspate. Reference to the degree of cuspation of a dentition is actually to the degree of cuspation of the most highly-cuspate teeth of that dentition. In spite of such

TABLE 2.—Degrees of cuspation

Species	Non-cus- pate	Low	Moder- ate	High	Very high
Sceloporus g. graciosus	.20	.45	.35	....	....
S. undulatus elongatus	.05	.65	.30	....	....
S. m. magister	.27	.47	.27	....	....
Uta s. stansburiana	....	.10	.66	.23	....
Urosaurus ornatus levis	.40	.45	.15	....	....
Crotaphytus c. collaris	....	.34	.39	.26	....
C. c. baileyi	....	.53	.28	.20	....
Gambelia wislizenii	....	.19	.37	.43	....
Holbrookia texana	.04	.56	.39	....	....
Callisaurus draconoides ventralis	.30	.60	.10	....	....
Phrynosoma platyrhinos	1.00	....	....	....	....
P. douglassii ornatissimum	1.00	....	....	....	....
P. cornutum	1.00	....	....	....	....
Dipsosaurus d. dorsalis	....	....	....	....	1.00
Sauromalus obesus	....	....	....	....	1.00
Ctenosaura similis	....	....	....	....	1.00

TABLE 3.—Position of most anterior cuspate tooth

Species	Anterior to 7	7-12	13-18	Posterior to 18
Sceloporus g. graciosus	.35	.30	.15	.20
S. undulatus elongatus	.10	.85	....	.05
S. m. magister	.27	.40	....	.33
Uta s. stansburiana	.24	.76	....	....
Urosaurus ornatus levis	....	.30	.30	.40
Crotaphytus c. collaris	.30	.69	....	....
C. c. baileyi	.14	.76	.10	....
Gambelia wislizenii	....	.86	.15	....
Holbrookia texana	.04	.78	.14	.04
Callisaurus draconoides ventralis	....	.45	.20	.35
Dipsosaurus d. dorsalis	1.00	....	....	....
Sauromalus obesus	.90	.10	....	....
Ctenosaura similis	1.00	....	....	....

TABLE 4.—Crown heights, crown widths, and position of highest and lowest teeth

Species	Maximum Snout-vent Length	Highest Teeth			Lowest Teeth	
		Crown Width	Position	Range of heights	Position	Range of heights
Sceloporus g. graciosus	63	.15-.20	1-3	.16-.48	10-12	.16-.38
S. undulatus elongatus	75-80	.25-.35	1-3	.32-.48	10-12	.20-.44
S. m. magister	140	.30-.40	1-3	.24-.64	10-12	.20-.44
Uta s. stansburiana	40-50	.15	4-6	.20-.36	10-12	.12-.28
Urosaurus ornatus levis	50	.10-.15	4-6	.20-.40	10-12	.16-.36
Crotaphytus c. collaris	120	.30-.60	1-3	.32-1.04	10-12	.32-.76
C. c. baileyi	120	.30-.60	1-3	.32-1.12	10-12	.28-.80
Gambelia wislizenii	120	.30-.50	1-3	.68-1.16	10-12	.48-.88
Holbrookia texana	60-70	.15-.25	13-15	.24-.40	1-3	.16-.40
Callisaurus draconoides ventralis	85	.15-.30	10-12	.20-.44	1-3	.16-.52
Phrynosoma platyrhinos	95	*	4-6	.32-.52	10-12	.32-.44
P. douglassii ornatissimum	84	.25-.30	1-3	.20-.44	13-15	.16-.40
P. cornutum	80-90	*	4-6	.20-.40	10-12	.16-.40
Dipsosaurus d. dorsalis	130	.25-.60	13-15	.44-.92	1-3	.32-1.04
Sauromalus obesus	200	.40-.80	1-3	1.12-1.32	16-18	.80-1.00
Ctenosaura similis	290	.30-.88	4-6	.60-.88	1-3	.48-.80

* Tooth proportions of P. platyrhinos and P. cornutum are essentially similar to those of P. douglassii ornatissimum.

gradation, however, position of the most anterior cuspate tooth is usually easily determined. Table 3 presents frequency of occurrence of the most anterior cuspate tooth in various positions in the maxilla. Positions are represented, at the head of each column, in terms of numbers of the teeth that limit them. Species of Phrynosoma are omitted from table 3 because their teeth are non-cuspate.

Dental measurements, including crown height and crown width, have been made by means of an ocular micrometer in a binocular dissecting microscope, calibrated to the nearest .04 mm. Crown height is the distance from the labial edge of the maxilla to the apex of the tooth, and crown width is measured at the widest part of the crown. Table 4 shows crown heights and positions of highest and lowest maxillary teeth, and approximate crown widths, for each species studied. Table 4 also includes approximate maximum snout-vent length, of each species, measured from tip of snout to anterior lip of cloaca (Smith, 1946). All measurements are recorded in millimeters.

As can be seen, crown heights are highly variable. Because of this variability, crown height, in itself, does not aid in discriminating between different dentitions. However, several of the species studied show slight but consistent differences in crown height at different regions of the jaw. Crown heights of the teeth of each individual have been plotted, as ordinates, against lengths of the dentate part of maxillae, as abscissas, on rectangular coordinate paper; in these plots vertical exaggeration is ten-fold. This procedure reveals the following types of maxillary dentition profiles:

TABLE 5.—Maxillary dentition and profiles

| | Anterior | | Highest teeth | | Teeth of Similar Height |
| | | | Middle | Posterior | |
Species	Abrupt decline	Gradual decline			
Sceloporus g. graciosus	.35	.50	....	....	.15
S. undulatus elongatus	.15	.60	....	....	.25
S. m. magister	.20	.67	....	....	.13
Uta s. stansburiana	.62	.14	....	....	.23
Urosaurus ornatus levis	....	.52	.09	.05	.33
Crotaphytus c. collaris	.35	.52	.04	....	.09
C. c. baileyi	.33	.52	....	....	.05
Gambelia wislizenii	.29	.62	....	....	.09
Holbrookia texana	....	.13	.09	.52	.26
Callisaurus draconoides ventralis	.10	.25	.20	.15	.30
Phrynosoma platyrhinos	....	.18	....	.27	.55
P. douglassii ornatissimum	.11	....	.33	....	.55
P. cornutum	....	.18	.18	.18	.45
Dipsosaurus d. dorsalis	....	.07	.07	.47	.40
Sauromalus obesus	....	.90	.10	---	....
Ctenosaura similis	....	....	.07	.53	.40

1. Region of highest teeth at anterior end of maxilla.
   a. Decline from highest to lowest teeth abrupt, and occurs anterior to middle of maxilla; teeth posterior to region of rapid decline of more or less equal height.
   b. Decline from highest to lowest teeth gradual rather than abrupt; in most cases it continues all the way to posterior end of tooth row.
2. Region of highest teeth in middle of maxilla; anterior and posterior teeth lower than middle teeth.
3. All teeth along maxilla of essentially the same height.
4. Region of highest teeth at posterior end of maxilla.

The differences in crown height, upon which these profiles are based, are small, and significance of such differences may be open to question. Nevertheless, the profiles themselves are consistent within certain species, and consideration of profile emphasizes position of high teeth, rather than differences in height between high and low teeth. Therefore it is felt that profile is a valid character for discriminating between dentitions.

Table 5 presents frequencies of different dentition profiles in the species under consideration. Headings of table 5 indicate the types of maxillary dentition profiles listed above.

Slenderness is described by the ratio, crown height divided by crown width. In larger lizards, posterior teeth are measurably wider than anterior; posterior teeth are probably wider in small individuals also, but the difference is too small to be measured by the means available (table 6).

Degree of lateral compression cannot be measured profitably. Differences can be observed in cleaned skulls, and, when well-developed, in preserved material. It is probable that lateral compression is directly related to degree of cuspation.

Tables 2 through 6 show dental characters which are subject to numerical

TABLE 6.—Approximate ranges of slenderness shown by teeth of each species

Species	Slenderness of teeth
Sceloporus g. graciosus	1.0-2.0
S. undulatus elongatus	1.0-1.6
S. m. magister	0.6-1.8
Uta s. stansburiana	1.5-2.5
Urosaurus ornatus levis	1.4-2.2
Crotaphytus c. collaris	0.6-2.2
C. c. baileyi	0.8-2.2
Gambelia wislizenii	1.4-2.8
Holbrookia texana	1.0-2.4
Callisaurus draconoides ventralis	1.2-2.2
Phrynosoma douglassii ornatissimum	0.5-1.5*
Dipsosaurus d. dorsalis	1.0-1.5
Sauromalus obesus	1.0-2.0
Ctenosaura similis	1.0-2.0

* Tooth proportions of *Phrynosoma platyrhinos* and *P. cornutum* are essentially similar to those of *P. douglassii ornatissimum*.

treatment. This includes degree of cuspation, position of most anterior cus-
pate tooth, crown height, profile, crown width, and slenderness. The follow-
ing section includes description of all characters that are not easily portrayed
in tabular form, such as differences in width of teeth in one individual, shape
of teeth, whether conical or cylindrical, sharpness, degree of lateral compres-
sion, and placement of teeth in maxilla. In addition, premaxillary teeth are
described for the cases in which their condition is unusual.

Sceloporus g. graciosus—differences in width of teeth along maxilla not distinguish-
able. Anterior teeth conical, rather sharp; posterior teeth more nearly cylindrical, with
roots of only slightly larger diameter than crowns. Very little lateral flattening of crowns
noticeable. Teeth fairly close-set in maxilla.

S. undulatus elongatus.—posterior teeth with slightly wider crowns than anterior teeth.
Front teeth blunter than those of *S. g. graciosus*. Similar to *graciosus* in other respects.

S. m. magister.—increase in crown width discernible in posterior teeth. Premaxillary
teeth blunt. Front teeth bluntly conical; recurved in many specimens. Most back teeth
blunt; when high-crowned appear "squared-off" in labial view. Back teeth usually low-
crowned, peg-like. Like other *Sceloporus* in situation of teeth in maxilla.

Uta s. stansburiana.—differences in crown widths along maxilla not distinguishable.
Teeth shaped like those of *S. g. graciosus* but sharper. Placement of teeth in maxilla as
in *Sceloporus*.

Urosaurus ornatus levis.—non-tabulated characters as in *Uta s. stansburiana*. See
tables 2 through 6 for differences.

Crotaphytus c. collaris.—increasing width of crowns from anterior to posterior of maxil-
la clearly measurable; posterior teeth about .1 mm wider than anterior teeth. Anterior
teeth conical, rather sharp, recurved. Posterior teeth show distinct lateral compression of
crowns at their apices, especially in individuals with high development of accessory cusps.
Roots greatly expanded, diameter greater than that of crowns; hence posterior teeth bluntly
conical rather than cylindrical. Teeth set in maxillary bone with roots very close together,
almost in contact with each other. Spaces between and around roots filled with bone.

C. c. baileyi.—non-tabulated characters as in *C. c. collaris*.

Gambelia wislizenii.—non-tabulated characters generally similar to those of *Crotophy-
tus*, with differences as follows: anterior teeth sharper and more strongly recurved; main
cusps of posterior teeth somewhat sharper; crowns of back teeth more laterally flattened at
apices, probably as a result of higher degree of cuspation.

Holbrookia texana.—slight increase in crown width from anterior to posterior distin-
guishable. Front teeth conical, blunter than those of *Sceloporus g. graciosus;* back teeth
cylindrical, with little or no expansion of roots. Lateral compression of crowns slight.
Situation of teeth in maxilla similar to that of *Sceloporus.*

Callisaurus draconoides ventralis.—increase in crown width from anterior to posterior
distinguishable; back teeth from .05 to .10 mm wider than front teeth. Shape of teeth simi-
lar to that of *Urosaurus*. Lateral compression and situation of teeth in maxilla similar to
conditions in *Holbrookia*.

Phrynosoma douglassii ornatissimum, P. platyrhinos, and *P. cornutum.*—increase in
crown width from anterior to posterior not distinguishable. All teeth more or less cylindri-
cal, blunt, low-crowned, and peglike; premaxillary teeth blunt. Many maxillary teeth mere
nubs, barely visible above the parapet. No lateral compression of crowns. Roots not
expanded. Teeth set very close together in maxilla, but no deposit of bone around roots.

Dipsosaurus d. dorsalis.—crowns of posterior teeth from .10 to .15 mm wider than
crowns of anterior teeth. All or nearly all teeth cuspate, but main cusps of front teeth
relatively larger than that of back teeth. Lateral compression of all teeth, including ante-
rior, very well-developed. Teeth have necks; roots constricted and teeth set quite far apart
in maxilla, but crowns flared so prominently in antero-posterior direction that they overlap.
Posterior margin of each flattened crown overlaps the anterior margin of its neighbor on
the labial surface. The posterior margin of each crown lies labially to the anterior margin
of its neighbor.

Sauromalus obesus.—premaxillary teeth with three cusps in many specimens. Increase
in width of crown toward posterior end of maxilla greater than in *Dipsosaurus;* in some
specimens back teeth are from .20 to .25 mm wider than front teeth. Lateral compression
well-developed, although first few teeth nearly conical in several specimens. Two to four

cusps anterior, and one accessory posterior to main cusp, instead of one anterior and one posterior as in all other species examined. In other characters similar to *Dipsosaurus.*

Ctenosaura similis.—posterior teeth about twice as wide as anterior. Not as many specimens with first few teeth nearly conical as in *Sauromalus,* more in that condition than in *Dipsosaurus.* In other characters similar to *Dipsosaurus.*

No conspicuous sexual differences have been observed in dentitions of any species in the present study. Apparent size differences include slight tendencies toward fewer teeth in the maxillary row and a higher degree of cuspation in smaller individuals, but neither is pronounced enough to be amenable to treatment by present methods.

DIET

GENERAL CONSIDERATIONS

The present study of lizard diet is based largely upon information contained in the literature rather than first-hand analysis of stomach contents, because of the great expenditure of time entailed by the latter procedure. An ideal sample for stomach analysis of any species should include numerous specimens collected throughout the greater part of the year, or of several years, in order to allow for seasonal variation in abundance of different potential food forms. Also, it should include specimens collected from different portions of the range of the species, and from whatever different environments in which the species may be found.

Accounts of lizard diet in the literature are varied, ranging from non-quantitative lists of insects present in stomachs examined, through rough estimates of percentage of the one or two most freqquent food animals present, to detailed lists in which the most frequent groups are identified to genus wherever possible, and in which numerical frequency is given for all groups present. The first two treatments of dietary data are by far the most common, and usually appear in connection with distributional, ecological, or taxonomic notes on various species. They are inadequate for basic purposes of the present study, and can be used only as supplementary information.

The third type of treatment, which constitutes almost the sole source of dietary information used in the present study, is unfortunately much less common than the other two types. It appears in accounts devoted to lizard diets *per se,* or in accounts concerned with the economic value of lizards as insect predators. More than half of the references used, involving three-quarters of the separate samples of lizards, are the work of G. F. Knowlton, to whom the present writer is deeply grateful for his care in recording and publishing the extensive details of lizard diet.

The ideal analysis of stomach contents should be based upon relative volume of various food animals present, as well as relative frequency, but it is doubtful whether direct volumetric treatment of stomach content, on a scale adequate to the scope of the present problem, would be accurate enough to make its application worthwhile. An approximate estimate of relative volume can be achieved by weighting frequencies of food animals by a factor proportionate to the cube of body length of the food animal. This involves identification of food fragments at least to family in most cases, and to genus in some, or identification to order or family, and estimate of body length of each food animal from its fragments. Lizards caught in the middle of the morning or around noon, depending upon season and locality, frequently have their

stomachs full of more or less entire bodies of insects; a sample consisting of such specimens would probably give the most nearly accurate estimate of relative quantity of different food animals for any given species.

Most investigators whose data are used in the present work have identified food animals to family, and many have carried the more common forms to genus wherever possible. Frequencies of each taxonomic category are given in terms of actual number present in all stomachs of each species examined. Rough comparisons can be made between diets of different samples on the basis of frequencies of food animals, but this method introduces a strong bias toward smaller forms in the diet. For example, in the total contents of the stomachs of five lizards, ten ants comprise a much smaller part than, say, ten grasshoppers, although the frequency is the same for each. To avoid such discrepancies, the present writer has estimated body length of each food animal listed in the literature; these estimates are then cubed in order to provide an estimate of volume, and used as weighting factors for the corresponding frequencies. The smallest identified food animals recorded in significant numbers in any diet are approximately 3 to 5 mm in body length. For arithmetical simplicity, this value is here considered as unity. Cubed body lengths are divided by 10 before multiplication by their respective frequencies, in order to prevent the final result from being too unwieldy.

Use of the cube of body length as an index of volume of food animals assumes that all forms found in lizard diets are of the same bodily proportions. This assumption is, of course, limited. The most common insects occurring in the diets studied, in order of numerical frequency, are ants, grasshoppers, leafbugs and leafhoppers, bees and wasps, and Lepidoptera (chiefly larvae). The described method of estimating volume tends to exaggerate the importance of slender forms. Caterpillars are in general more slender than grasshoppers; therefore, in the weighted dietary data which follow, the percentage of stomach contents by volume contributed by caterpillars is probably exaggerated, as compared with that contributed by stouter forms. The percentage contributed by ants is perhaps even more highly exaggerated, since in addition to their being of rather slender body form, the peculiarly pinched-in region of the anterior abdomen in these animals probably reduces their body volume considerably, with respect to body length. Grasshoppers are probably of somewhat stouter body form than most caterpillars; they are almost certainly of greater volume with respect to length than are ants. Bees and wasps are probably also of greater volume with respect to length than are caterpillars or ants, in spite of the presence of some thin-waisted forms like *Polistes*. Thus the exaggeration of percentage by volume of caterpillars and ants is at the expense of that of grasshoppers, and bees and wasps, in diets in which slender and stout forms occur together. Bodily proportions of leafbugs and leafhoppers are probably more nearly similar to those of grasshoppers than to those of other insects encountered. It is admitted that use of cubed body length as an index of volume is no more than a crude approximation, and no pretense of accuracy is intended, but even in source material in which taxonomic identification has not been extended below family, the above treatment affords a clearer idea of the true composition of any diet than does examination of unweighted numerical frequencies.

Probably the simplest method for comparison of stomach contents of

various species of lizards is by means of their compositions in terms of taxonomic categories of food animals. The objection to this approach is that comparison of frequencies of taxonomic categories as such offers no direct clue to the physical nature of dietary components, and hence to possible selective effects of diet upon dentition. In an attempt to bring out more clearly the characteristics of diet that might influence function of dentition in any lizard, the following scheme has been devised.

Food animals, which in most of the lizard under discussion consist chiefly of insects, are arranged according to their activity and the resistance of their integument. Three degrees of activity are recognized, and designated as high, intermediate, and low; three degrees of integumentary weight are recognized, and designated as light, intermediate, and heavy. Taxonomic categories falling into these "functional categories" are listed in table 7. The list is not complete, but it contains all taxonomic groups that occur in greatest numbers of individuals in recorded lizard diets. In addition, it contains taxonomic groups whose members are believed to show best the characteristics of the functional categories in which they are placed.

The term "active" as used here does not refer to the intrinsic activity of an animal, but rather to the potential activity shown upon threat of capture, or upon being captured by a lizard, in relation to the predatory equipment of the lizard. For example, an ant is not less intrinsically active than is a leafhopper of the same size, but the leafhopper is a strong jumper, while the ant is not. It is expected that the ant, when captured by a lizard, will be subdued by salivary or mucous secretions of the lizard's mouth, without important intervention by the predator's dentition. Many, perhaps most, lizards that eat considerable quantities of ants, lap them up with their tongues; if the lizard misses an ant at the first try, the victim has moved only a short distance before the lizard has a chance to try again. The leafhopper, on the other hand, must in all probability be captured by a quick snap of the teeth; if the lizard misses in its first attack, the leafhopper moves well beyond reach in escaping, and the predator must hunt for a fresh victim. Even after being captured, the leafhopper may be able to escape, because of its ability to jump, while the lizard is still trying to swallow it, unless the victim has been subdued by having been bitten. Thus it is probable that dentition plays a more important role in the capture of the leafhopper than in the capture of the ant, and leafhoppers are considered to be of intermediate activity, while ants are considered to be of low activity.

A rough correlation is evident, in this functional classification, between degree of activity of the food animal in relation to the predator, and the size of the food animal. The assumption behind this arrangement is that the larger the food animal, the better its chances of escaping the grip of the predator. The correlation is particularly apparent in the case of the beetles; in general, those of less than 10 mm body-length are classified as passive, and those of more than 10 mm body-length as of intermediate activity. Larval Lepidoptera are probably less active intrinsically than, for example, ants, which are here considered functionally passive. The classification of caterpillars as of intermediate activity is based chiefly on the fact that most of them are larger than most ants; the fact that they are also more flexible may also enter the picture to some extent. With respect to very small lizards of

the present series, food animals ordinarily classified as of intermediate activity, may be equivalent to forms that are active with respect to larger lizards. This possibility is discussed in greater detail in a later section of this paper, in which the diet of *Uta s. stansburiana* is compared with that of other lizards.

Most food animals classified as active are among the largest forms recorded in lizard diet. In addition, many of them are strong fliers, like bees and wasps, or strong jumpers, like grasshoppers.

Functional categories may be defined on the basis of activity in the following general manner. Passive forms are those that can be subdued by oral secretions of the predator, without use of the teeth. Frequently they may be captured by use of the tongue alone. Forms of intermediate activity must be bitten in order to be subdued; securing them requires the assistance of the teeth, if only in the initial seizure. Small forms that are classified as of intermediate activity are strong jumpers or fliers. Food animals classified as active must be chewed or otherwise injured to some extent, in order to be subdued sufficiently for swallowing; in other words, the predator must use its teeth more than merely for initial seizure. Lizards do not always crush large, active forms in

TABLE 7.—Integumentary weight and activity of food animals*

Degree of Activity	Weight of Integument		
	Light	Intermediate	Heavy
High	Phasmids, mantids roaches; adult Lepidoptera; large spiders; crane flies (Tipulidae)	Orthoptera, except those listed under "high-light"; adult braconids and ichneumons; adult horseflies (Tabanidae) and syrphid flies	Adult bees, andrenids, sphecids, vespids, and chrysidids; adult robber flies (Asilidae); Odonata; centipedes
Intermediate	Leafbugs (Miridae and Lygaeidae), Nabidae; adult Diptera such as *Drosophila* or *Culex*; caterpillars; adult Neuroptera	Leafhoppers (particularly *Eutettix* and *Agallia*), planthoppers (Fulgoridae), squash bugs (Coreidae); adult Diptera such as muscids, sarcophagids, and tachinids; meloid beetles and larger caribids	Pentatomids, cercopids, treehoppers (Membracidae) reduviids; larger weevils and tenebrionids, elaters, scarabs, larger buprestids
Low	Aphids; termites; thrips; larval Diptera; lacebugs (Tingiidae); larval Hymenoptera; larval Neuroptera; Corrodentia	Ants; Collenbola; small carabids, staphylinids; blackflies	Most weevils, coccinellids, chrysomelids, buprestids, dermestids, small tenebrionids

* It should be noted that relative integumentary weight and activity of the insect prey, as listed in this table, refer specifically to the function of these attributes with respect to lizard predators, as explained in the text.

order to swallow them; often, having seized active insects, they hold them in their teeth and shake them violently, or beat them on the ground.

Classification of food animals according to weight of integument is, like classification according to activity, largely a matter of personal judgment. The assumptions upon which classification is based are probably best illustrated by the list of taxonomic categories included under each functional category defined by weight of integument (see table 7).

Some light is thrown on the function of lizard dentition in handling integuments of different weight, by examination of the stomach content of 22 specimens of *Crotaphytus c. collaris* and 32 specimens of *Holbrookia texana*. In these samples, many remains of food animals show the marks of teeth. In forms with integument in the "heavy" category, such as chrysomelids, coccinellids, buprestids, weevils, and scarabs, and scutellarid and pentatomid bugs, the elytra and scutella break in clean cracks, like an egg, without crushing or crumpling. Many of these fragments have neat holes punched in them, presumably by the teeth of the lizard; two fragments show three holes in a straight line, and several have two holes apiece. In forms with integument in the "interemdiate" category, such as most of the carabids, elytra more often exhibit crushed and partially cracked regions than they do clean breaks; some fragments are found with holes in them. Crushed regions are restricted to only a part of each fragment and are usually linear in configuration; this fact, and the presence of linearly-arranged holes in the harder food fragments, are interpreted as evidence that damage to such resistant material is done by the dentition of the predator, rather than by peristalsis after the food has been swallowed. This interpretation is supported by the presence of few more unbroken elytra, scutella, and other hard parts in the stomach than in the intestine, the contents of which have been subjected to peristalsis for a longer time than have the contents of the stomach.

The bodies of animals with integument in the "light" category, such as Lepidoptera, phasmids, mantids, etc., are often found crumpled up, accordion fashion, but unbroken. When such remains are unfolded, the integument is seen to be sound and entire; no pierced specimens of this category were found in the samples examined by the writer. Probably the initial seizure, plus chewing motions involved in swallowing, play an important part in crumpling such specimens, but there is no evidence to show that peristalsis does not play an equally important part in their reduction.

Size enters the relation between weight of integument of the food animal, and the dentition of the lizard, when the food animal is so small that tongue and saliva of the lizard are sufficient to subdue the prey without use of the teeth. Thus weight of integument is probably of minor importance in small food animals in the passive category, becoming almost nil in form such as thrips, Corrodentia, Collembola, etc., which are placed there entirely because of their small size. Another way in which size enters the picture is in the proportionate increase in strength of an object of given shape and composition, with reduction in size; of two food animals with integuments of similar nature, the smaller will present more resistance to lizard dentitions. However, at the level of the present study, the effects of this relation are obscure and difficult to approach, and therefore are not being taken into consideration.

Diets of most or all of the insect-eating lizards discussed in this paper

contain a certain amount of vegetable material. Most of this component is accidental, having been ingested with insect prey. In some forms, a part may reflect the habit of eating tender vegetation occasionally, especially in spring. No attempt is made to compare the vegetable component of predominantly insect diets, because in those that have been studied, vegetation makes up an insignificant amount, 5% or less. Vertebrates are also present in some diets. They are difficult to treat in the manner in which insects have been dealt with above, and are considered independently in the following descriptive and comparative sections of the paper.

DESCRIPTIONS OF VARIOUS DIETS

Table 8 presents the composition of diet of each species of insectivorous lizard in the present series, in terms of percentage of functional categories in each diet. Percentages of functional categories are based upon weighted frequencies of food animals in the total stomach content of all available samples of each species.

TABLE 8.—Composition of lizard diets in terms of functional categories

Species	High Activity			Intermediate Activity Integument			Low Activity		
	L*	I	H	L	I	H	L	I	H
Sceloporus g. graciosus	.03	.34	.04	.02	0.9	.01	.01	.42	.03
S. undulatus elongatus	.05	.10	.15	.11	.09	.04	.01	.43	.03
S. m. magister	.01	.04	.03	.22	.04	....	....	.61	.01
Uta s. stansburiana	.07	.19	.09	.15	.26	.05	.02	.17	....
Urosaurus ornatus levis	.11	.10	.38	.14	.17	.01	.01	.05	.03
Crotaphytus c. collaris	.05	.87	.03	.01	.02	.02	....	....	....
C. c. baileyi	.06	.51	.11	.19	.04	.06	....	.01	.01
Gambelia wislizenii	.04	.80	.04	.07	.02	....	....	.02	....
Holbrookia texana	.18	.35	.10	.10	.08	.05	.04	.03	.04
Callisaurus draconoides ventralis	.09	.08	.40	.35	.05	.01	.01	.02	.01
Phrynosoma platyrhinos	....	....	.01	.04	.01	....	....	.93	....
P. douglassii ornatissimum	.01	....	....	.01	....	....	....	.96	....
P. cornutum	.01	....	.02	.02	.05	.01	....	.88	....

* L—light; I—intermediate; H—heavy.

Sceloporus g. graciosus (Cole, 1932; Knowlton, 1938, 1942, 1946, 1947; Knowlton and Janes, 1932, 1933; Knowlton and Thomas, 1936; Pack, 1921).—the diet of *S. g. graciosus* is remarkably uniform, consisting chiefly of ants (low activity, intermediate integument) and grasshoppers (high activity, intermediate integument). Weighted frequency of ants is slightly greater than that of grasshoppers, but since the weighting method used in this study tends to exaggerate the importance of ants in any diet, it is probable that the two forms are actually of equal importance. Seasonal and environmenal differences appear to be minor.

Sceloporus undulatus elongatus (Knowlton, 1934, 1937; Woodbury, 1932).—the diet of *S. u. elongatus* is fairly uniform, so far as can be determined from limited evidence. Ants (low activity, intermediate integument), although their importance is somewhat exaggerated, are the most important single category. The remainder of the diet is varied, and is made up in general of forms which are more active and heavily armored than ants. No data concerning seasonal and environmental variation are available for this species.

Sceloporus m. magister (Knowlton, 1934, 1938).—the bulk of the diet of this form

consists of ants (low activity, intermediate integument), and most of the remainder of caterpillars (intermediate activity, light integument). Proportions are similar in both available samples.

Smith (1939), in a non-quantitative report on a sample of *S. m. magister*, mentions the presence of several lizards and a toad in the stomachs. His data and that of Ruthven (1907) agree with the above indication that ants make up the bulk of the diet. They also list considerable quantities of plant material.

Uta s. stansburiana (Cole, 1932 identified as *Urosaurus ornatus levis* by Cole; Smith (1946) assigns Cole's specimens to *U. s. stansburiana*: Knowlton, 1938; Knowlton and Anthon, 1935; Knowlton, Fronk, and Maddock, 1942; Knowlton and Janes, 1932; Knowlton and Thomas, 1936).—the diet of *U. s. stansburiana* is highly varied, consisting in general of approximately equal parts of leafhoppers (intermediate activity, intermediate integument), grasshoppers (high activity, intermediate integument), ants (low activity, intermediate integument), leafbugs and caterpillars (intermediate activity, light integument) and occasionally bees and wasps (high activity, heavy integument). Ants are probably not as important as in any species of *Sceloporus*. The diet of *U. s. stansburiana* is also quite variable, specimens collected from Russian thistle containing mostly leafhoppers and ants, and those collected from sage-brush flats containing mostly grasshoppers and leafbugs. Seasonal variation of diet appears to be pronounced, grasshoppers being common in diet early in the year, and ants and leafhoppers later on. Summer diet is varied, consisting of most of the above groups in approximately equal quantities. Much of this variation is undoubtedly due to differences in abundance of various food animals at different times and in different places.

Urosaurus ornatus levis (Knowlton, 1934, 1938).—the most abundant animals in the diet of this lizard are bees and wasps (high activity, heavy integument). Second in importance are leafhoppers, and Diptera like Calliphoridae and Muscidae (intermediate activity, intermediate integument) and leafbugs and caterpillars (intermediate activity, light integument). Third are spiders (high activity, light integument) and grasshoppers (high activity, intermediate integument). Other functional categories, including that of low activity and intermediate integument, are negligible. Data regarding seasonal and environmental variation are not available.

Crotaphytus c. collaris (Blair and Blair, 1941; Burt, 1928).—twenty-two individuals collected and examined by the present writer. The diet of *C. c. collaris* appears to consist very largely of grasshoppers (high activity, intermediate integument) for most of the year, except in early spring, when a part of the grasshopper component is substituted by Lepidoptera (high or intermediate activity, light integument), larger Coleoptera (intermediate activity, heavy integument), and larger flying Hymenoptera (high activity, heavy integument). Lizards are also present in appreciable quantities.

Crotaphytus collaris baileyi (Camp, 1916; Knwolton, 1934, 1938; Knowlton and Thomas, 1936; Pack, 1923a).—the diet of this lizard consists chiefly of grasshoppers (high activity, intermediate integument). Minor components are caterpillars (intermediate activity, light integument) and bees and wasps (high activity, heavy integument). Adult Lepidoptera and large spiders (high activity, light integument) and larger beetles (intermediate activity, heavy integument) are also present. *C. c. baileyi* is reported to eat other lizards occasionally. No data are available regarding seasonal variation bf diet.

Gambelia wislizenii (Knowlton, 1934, 1938; Knowlton and Thomas, 1936; Pack, 1922).—the diet of *G. wislizenii* consists almost entirely of grasshoppers (high activity, intermediate integument) throughout the greater part of the year. There is some evidence that bees and wasps (high activity, heavy integument), adult Lepidoptera (high activity, light integument), and miscellaneous forms of intermediate activity and integument may replace grasshoppers in the diet of *Gambelia* during the early part of the season.

Other lizards are often found in the stomachs of specimens of *G. wislizenii*; twenty-three are reported from the samples reviewed here. Non-quantitative reports of lizards being found in *G. wislizenii* stomachs are by Little and Keller (1937), Camp (1916), and Ruthven (1907).

Holbrookia texana.—the only available quantitative data on the diet of this species are based upon a sample of 32 lizards collected by the present writer. Grasshoppers (high activity, intermediate integument) are first in importance in the diet of this sample, large spiders and adult Lepidoptera (high activity, light integument) are second, and bees and wasps (high activity, heavy integument) and caterpillars and leafbugs (intermediate activ-

ity, light integument) are third. Various beetles (intermediate to low activity, intermediate to heavy integument) are present in considerable number; ants (low activity, intermediate integument) make up the smallest portion of the diet. Non-quantitative reports by Burt (1928) and Hartman (1906), on the diet of various subspecies of *H. maculata*, mention grasshoppers as the most important group of food animals. Ruthven (1907) lists grasshoppers as the most important prey in *H. m. maculata*, but not among the three most important forms in *H. m. flavilenta*. The dietary difference observed by Ruthven is difficult to evaluate, but the bulk of evidence indicates that grasshoppers are important in the diet of *Holbrookia*.

Callisaurus draconoides ventralis (Knowlton, 1938; Knowlton and Smith, 1935; Pack, 1923).—the bulk of the diet of this lizard consists of bees, wasps, robberflies, etc. (high activity, heavy integument) and caterpillars (intermediate activity, light integument). The former group is probably the more important. Grasshoppers (high activity, intermediate integument) and large spiders (high activity, light integument) appear with moderate frequency. Beetles (intermediate activity, heavy integument) are also present, but ants (low activity, intermediate integument) appear relatively rarely. Data on seasonal and environmental variation are lacking.

Phrynosoma douglassii ornatissimum, P. platyrhinos, and *P. cornutum.*—quantitative data show that in general, the diet of these three species consists almost entirely of ants (low activity, intermediate integument); ants make up more than 85% of the diet of samples investigated by Knowlton (1934, 1942), by Knowlton and Janes (1932), Knowlton and Thomas (1936), and by the present writer. Non-quantitative data corroborate this conclusion (Burt, 1928; Camp, 1916; Ruthven, 1907): singly collected individuals, or numerous members of a sample, are usually reported as being gorged with ants. Rarely, individuals are found to be as gorged with small beetles as others are with ants (Hartman, 1906); this is probably of only slight significance, and it is safe to say that *Phrynosoma* has a very uniform diet, which consists essentially of ants and nothing much else.

Dipsosaurus d. dorsalis, Sauromalus obesus, Ctenosaura similis.—numerous scattered observations agree that these genera are herbivorous in habit. This does not mean that their diet is entirely restricted to vegetable material; species of *Ctenosaura* have been reported to include animals in their diet at times. It does not mean that the great bulk of the diet of these lizards consists of plants; they eat far more vegetable material than any other lizard discussed in this paper.

COMPARISON AND GROUPING
DIET

Most samples of stomach contents of a single species are more similar to each other than they are to samples of other species, but an occasional sample appears rather drastically different from others of the same species. Such different samples are usually those which have been collected in the spring, and the differences can be ascribed to seasonal variation. However, of the samples available for the present study, only those collected very early in the year show spectacular differences; through most of the season during which lizards are active, stomach contents of samples of a single species are similar. The diet upon which a species subsists through the greater part of the year probably exerts the greatest selective effect upon dentition.

Samples of a single species collected from different environments often exhibit differences in diet also, but these differences are relatively minor in most cases; they are much less pronounced than seasonal differences. A species like *U. s. stansburiana* or *S. g. graciosus*, which has been collected in numbers from two different environments, occurs in much greater numbers in one environment than in the other. The environment in which the greater number of individuals is found can probably be considered as the one to which the species is better adapted, in diet as well as in other respects; individuals are found outside of it only as a result of their random wandering.

Available information indicates that in most of the lizards under discussion,

one or two predominant functional categories of food animals make up a much greater part of the diet than do all other categories together.   These predominant functional categories in turn consist of a few families of a single order of insects, except in the herbivorous lizards.   The diet of the herbivorous lizards is considered to consist of a single functional category because it consists almost exclusively of buds, leaves, and blossoms, chiefly of herbaceous plants; finer subdivision of vegetable diet is not feasible, since information upon which it might be based is lacking.

Lizards in the present series can be placed in the following five groups, on the basis of diet:

1.   Diet chiefly or exclusively of vegetable material. Includes *Dipsosaurus d. dorsalis Sauromalus obesus*, and *Ctenosaura similis*.

2.   Food animals chiefly of low activity, intermediate integument (ants).   Includes *Phrynosoma platyrhinos*, *P. douglassii ornatissimum*, *P. cornutum*, *Sceloporus m. magister*, and *S. undulatus elongatus*.

3.   Food animals chiefly of high activity, intermediate integument (grasshoppers). Includes *Crotaphytus c. collaris*, *C. c. baileyi*, *Gambelia wislizenii*, *Holbrookia texana*, and *Sceloporus g. graciosus*.

4.   Diet highly varied; resembles that of group 3 in some respects and that of group 5 in others, but is distinctive in the relatively high proportion of food animals of intermediate activity, intermediate integument (mostly leafhoppers) which it contains. Sole member of group 4 studied is *Uta s. stansburiana*.

5.   Diet rather varied; most important functional category consists of food animals of high activity, heavy integument (bees and wasps).   Food animals of intermediate activity, light integument (caterpillars and leafbugs), of high activity, intermediate integument (grasshoppers), and of high activity, light integument (adult Lepidoptera and large spiders) also present in varying but probably significant amounts. Group 5 includes *Callisaurus draconoides ventralis* and *Urosaurus ornatus levis*.

No further comment on group 1 is necessary.

The three species of *Phrynosoma* are typical of group 2, since their diet consists of ants and very little else. *Sceloporus m. magister* is placed in group 2 because ants comprise 60% or more of its diet; exaggeration of the importance of ants, through the method of weighting used here, does not nullify the fact that ants are by far the most important single group of food animals in the diet of *S. m. magister*.   The presence of caterpillars in the diet of *magister* can be interpreted as a tendency toward the condition found in groups 4 and 5.   The place of *S. undulatus elongatus* in group 2 is less distinct than that of *magister*.   Although ants compose 40% to 50% of the diet of *undulatus*, active forms make up nearly all of the remainder; the importance of ants is somewhat exaggerated at the expense of most of the more active forms.   *S. undulatus elongatus* is placed in group 2 with the reservation that it shows a distinctly greater tendency to prey on active forms than do other members of the group.

Crotaphytus c. collaris, *C. c. baileyi*, and *Gambelia wislizenii* are typical of group 3; in general, food animals of high activity, intermediate integument (grasshoppers) make up from 50% to 90% of the diet of these forms.   This functional category may be greatly reduced in the spring; at that time it appears to be replaced, in the diet of all three lizards, by food animals of high and intermediate activity, light integument (adult and larval Lepidoptera, respectively), by food animals of high activity, heavy integument (bees, wasps, etc.), or by different combinations of these categories. Vertebrates comprise an appreciable part of the diet of *G. wislizenii*; *C. c. collaris* and *C. c. baileyi* also in-

clude vertebrates in their diet, but not to the extent to which G. *wislizenii* does. *Sceloporus m. magister* is the only other lizard in the series which preys on vertebrates to any extent; its consumption of them is smaller than is that of *Crotaphytus* or *Gambelia*.

Grasshoppers comprise the most important single category in the diet of *Holbrookia texana*, at about 35%; other categories include food animals of high activity, light and heavy integument, and of intermediate activity, light integument, as in the spring-time diet of *Crotaphytus* and *Gambelia*. It is suggestive that the only quantitative data concerning the diet of *Holbrookia* were collected in the spring.

The diet of *Sceloporus g. graciosus* is peculiar in that it consists of approximately equal parts of grasshoppers and ants (35%-40% each). Placing *graciosus* in group 3 is more or less arbitrary, and it could as well be placed in group 2. Since members of group 2 eat mostly ants and practically no grasshoppers, and since in members of group 3 this condition is almost exactly reversed, the diet of *S. g. graciosus* constitutes an ideal transition between the two groups.

The diet of *Uta s. stansburiana*, sole investigated member of group 4 is peculiar in that food animals of intermediate activity and integument (mostly leafhoppers) predominate slightly, at 25%, over other categories. Other important categories are those composed of food animals of high activity, intermediate integument (grasshoppers) and of low activity, intermediate integument (ants), at 15% to 20% each; in this respect the diet of *U. s. stansburiana* resembles that of *Sceloporus g. graciosus*, although quantities of both functional categories are smaller in the diet of *Uta*. Ants, especially, are less important in the diet of *Uta*. Although their weighted frequency is smaller in samples of *Uta* than in samples of *Sceloporus*, their variation from sample to sample is greater. Food animals of high activity, heavy integument (bees, wasps, etc.) and of intermediate activity, light integument (leafbugs and caterpillars) are also present in significant amounts (10%-15%).

The total number of active forms in the diet of *U. s. stansburiana* is about the same as that in the diet of *S. g. graciosus*. In addition, about 45% of the diet of *Uta* consists of forms of intermediate activity, mostly leafhoppers. Leafhoppers are placed in the category of intermediate activity chiefly because of their small size; they are probably as active intrinsically as grasshoppers. It is possible that with respect to a lizard like *U. s. stansburiana*, the smallest of the series, leafhoppers should be considered as of high rather than of intermediate activity. This possibility tends greatly to increase the resemblance of the diet of *Uta* to that of *Crotaphytus* and *Gambelia*.

The most important food category in the diet of group 5 consists of animals of high activity, heavy integument (bees, wasps, etc.), at about 40%. The diet of *Callisaurus draconoides ventralis* contains in addition about 35% of food animals of intermediate activity, light integument (caterpillars), and that of *Urosaurus ornatus levis* about 15% each of food animals of intermediate activity, intermediate integument (mostly leafhoppers), and of intermediate activity, light integument. Diet of both lizards contain about 10% each of animals of high activity, light integument (mostly adult Lepidoptera, some large spiders) and of high activity, intermediate integument (grasshoppers). Diet of group 5 is somewhat similar to the springtime diet of *Crotaphytus* and

Gambelia (group 3); it is also similar to the general diet of these genera in its relatively insignificant proportion of ants, although the predominant functional categories of groups 3 and 5 separate them rather distinctly.

DENTITION

In general, the following five groups of dentitions correspond with the five groups based upon diet, discussed in the preceding section. Each is based upon typical members of one of the diet-based groups: Group A is based upon *Dipsosaurus d. dorsalis, Sauromalus obesus,* and *Ctenosaura similis;* group B upon three species of *Phrynosoma;* group C upon the two subspecies of *Crotaphytus collaris;* group D upon *Uta s. stansburiana;* and group E upon *Urosaurus ornatus levis* and *Callisaurus draconoides ventralis.*

Group A.—Teeth highly to very highly cuspate; first cuspate tooth near or at anterior end of maxilla. Teeth laterally compressed, so that crowns are slender labio-lingually but broad antero-posteriorly; crowns sharp, blade-like. Profile variable, but line drawn through apices of crowns is even.

Group B.—Teeth poorly or not at all cuspate, stout, bluntly conical or peglike. Profile variable, obscure; crown line uneven. No lateral compression.

Group C.—Teeth moderately to highly cuspate, first cuspate tooth about midway along maxilla. Teeth are rather stout and broad-based, but conical and sharper than those of group B. Front teeth tend to be abruptly higher than back teeth, sharper, and more conical. When difference between front and back teeth is well-developed, the lizard appears heterodont. This condition is still better developed in group D. Slight lateral compression, restricted to apices of crowns.

Group D.—Teeth rather highly cuspate; first cuspate tooth anterior to middle of maxilla. Front teeth slender, sharp, conical; have a strong tendency to be abruptly higher than back teeth, more so than in any other species studied. Little or no lateral compression of crowns.

Group E.—Teeth poorly cuspate; first cuspate tooth usually posterior to middle of maxilla. Teeth slender, rather cylindrical up to apex of crown, where they taper quickly to sharp point. Profile somewhat variable, posterior teeth in general as high as anterior teeth. Little or no lateral compression of crowns.

DIET AND DENTITION

Dentitions of group A are distinguished from all other dentitions in the series by the high degree of lateral flattening exhibited by the teeth, and by the blade-like cutting edges of the crowns. The first cuspate tooth is further anterior than in any other form, and the teeth are more highly cuspate. All members of group A are entirely herbivorous.

Dentitions of group B are distinguished from others by extremes of bluntness, stoutness, and lack of cuspation, exhibited by teeth of the three species of *Phrynosoma.* All species of *Phrynosoma* studied subsist almost entirely upon ants.

Dentitions of group C are distinguished by teeth which are moderately to highly cuspate, stoutly conical, and rather sharp. The "heterodonty" described above is well-developed in the typical members of the group, *Crotaphytus c. collaris* and *C. c. baileyi.* Diets of these two subspecies are very similar, consisting largely of grasshoppers.

Dentitions of the three species of *Sceloporus* suggest a graded series between groups B and C. *S. m. magister* has the stoutest, bluntest, and least cuspate teeth, approaching closely the condition found in *Phrynosoma* in these respects. The teeth of *S. g. graciosus,* on the other hand, are more slender, sharper, and more highly cuspate than those of *magister,* and approach the condition of *Crotaphytus.* In slenderness, sharpness, and degree of cuspa-

tion, *undulatus* is about midway between *magister* and *graciosus*, in position of first cuspate tooth it tends more to resemble *Crotaphytus*. The profile is similar in all three species of *Sceloporus*, but *graciosus* exhibits a perceptibly greater tendency for the front teeth to be abruptly higher than the back, instead of gently higher, as in *magister* and *undulatus*. In *magister*, the greater part (about 60%) of the diet consists of ants; in *undulatus* ants are the predominant single category in the diet, but they make up less than half of it; in *graciosus*, grasshoppers are as important as ants, the two comprising about 40-60% of the diet.

The dentition of *Uta s. stansburiana*, the sole member of group D, resembles that of group C in degree of cuspation and position of first cuspate tooth, and group E in slenderness and sharpness. It exhibits a greater tendency to have anterior teeth abruptly higher than posterior teeth, than do other forms. The diet of *U. s. stansburiana* is distinctive in that the most important single constituent is leafhoppers. In containing ants and grasshoppers in significant amounts, the diet resembles that of *Sceloporus g. graciosus;* if the leafhopper component of the diet is considered as belonging to the active functional category on account of the small size of *stansburiana*, the diet resembles that of *Crotaphytus* even more closely. The presence of bees and wasps in the diet indicates a resemblance to the diet of group E.

The dentition of *Gambelia wislizenii* resembles that of *Uta s. stansburiana* more than any other in the present study. The teeth are of somewhat higher degree of cuspation than are those of *Uta*, but are about the same in position of first cuspate tooth, slenderness and sharpness. They resemble teeth of *Crotaphytus* more closely in broadness of root and in profile. Diet is essentially similar to that of *Crotaphytus*, but includes a considerable greater proportion of vertebrates.

Teeth of *Holbrookia texana* are more highly cuspate than are those of *Sceloporus g. graciosus*, less so than those of *Crotaphytus;* they are about as sharp as those of *S. undulatus*, and as slender as teeth of group D and E. In profile the dentition is similar to that of group D. The rather meagre data on diet indicate that *Holbrookia* subsists chiefly upon grasshoppers, large spiders, and adult Lepidoptera; significant amounts of bees and wasps, and caterpillars are also present. Ants are unimportant.

Dentition of group E are distinguished by their slender, rather cylindrical, sharp teeth. Cuspation is better developed than in group B but not as well as in group C. In *Callisaurus draconoides ventralis* the profile is slightly more variable than in *Urosaurus ornatus levis*, but this is a minor difference; in both, the posterior teeth are about as high as the anterior. Diet of *Callisaurus* and *Urosaurus* is distinctive in that the most important component consists of bees and wasps, etc., and also in that grasshoppers are of relatively slight importance, and ants of none at all.

DISCUSSION AND CONCLUSION

Food animals of different degree of activity and weights of integument may be expected to exert different selective influences upon dentitions of their lizard predators. Large, active, or heavily armored animals require the use of teeth in their capture. Large forms like caterpillars must be seized with the teeth, and the teeth are probably also employed to a considerable extent in manuevering them into position for swallowing. Grasshoppers, because of their ability

to leap, must be seized quickly and held firmly during violent exertions required to subdue them. Because grasshoppers are not heavily armored, their predation probably requires little more than a holding function of the teeth of the predator. Predation of a heavily-armored, active form like a bee or a wasp requires the same use of the teeth in holding, and in addition perhaps a rudimentary chewing activity, in order to injure the prey through its armor. It is doubtful whether the shaking or pounding treatment, which lizards use to subdue grasshoppers and other large forms, would be as effective as chewing, to subdue a heavily-armored form. In addition, most bees or wasps must be dispatched quickly in order to nullify the sting, which if not dangerous to the predator, is at least uncomfortable; chewing is probably quicker in subduing prey than is shaking or pounding.

Unlike the foregoing food animals, ants can probably be seized and subdued with but minimal use of the teeth, since because of their small size and inability to jump or fly, oral secretions of the predator are adequate for their disposal. Also, because of their small size, ants are swallowed whole, and what armor they possess offers no problem to the predator.

No attempt is made in this study to work out the details of dental adaptation to diet. However, the agreement of dentition with diet, described in the preceding section, indicates certain broad lines of dental adaptation which are probably ascribable to selection through the medium of diet. For example, it is permissible to speculate that the conical, high-crowned front teeth of a form like *Crotaphytus* are adaptive to the necessity of dealing with relatively large and active, but only moderately armored food animals. A form like *Callisaurus* is probably also adapted to dealing with large and active prey, but in its case much of the prey is more heavily armored than is that of *Crotaphytus*. If chewing is necessary to subdue heavily armored, active food animals quickly, a dentition having high-crowned posterior teeth as well as high-crowned anterior teeth might prove advantageous, in that more teeth would come to bear on the prey at one time.

Why high-crowned back teeth should not be as advantageous for *Crotaphytus* as for *Callisaurus* is obscure. It is possible that high-crowned front teeth are advantageous for the initial quick seizure of prey, while high-crowned back teeth make for a slightly slower attack and are therefore an actual disadvantage in dealing with an animal like a grasshopper, which is capable of sudden leaps.

The function of the teeth of *Phrynosoma*, which feeds chiefly upon ants, is less obvious than is the function of the teeth of lizards which feed upon more active insects. Because of the great difference in size and activity between ants and such insects as grasshoppers, or bees and wasps, it is probable that selection through the medium of a diet consisting mainly of ants operates in a different direction than does selection through a diet of grasshoppers, or a diet of bees and wasps. Therefore, the differences observed between the dentition of *Phrynosoma* and that of *Crotaphytus* or *Callisaurus* are interpreted as adaptation to different diets.

In spite of the great preponderance of ants in the diet of *Sceloporus m. magister*, which has apparently selected for blunt, poorly-cuspate teeth, the influence of a minority of more active forms is noticeable in the profile, which resembles that of lizards with diets of generally more active food animals. A diet consisting chiefly of ants has no selective tendency toward a heterodont

dental profile, if the dentition of *Phrynosoma* is any indication. The more active component of the diet of *magister*, which presumably does exert a selective influence toward such a profile, consists of caterpillars and vertebrates.

Leaves and blossoms are usually whole when found in lizard stomachs. Stems appear neatly clipped, and when the leaves themselves are damaged they appear cut, as though by shears, rather than torn. Thus it appears that teeth of herbivorous lizards act as shears, for cutting plant material, instead of merely as devices for gripping leaves or buds to tear them from the plant. The sharp, blade-like, almost serrate teeth of the herbivorous lizards studied appear well adapted to a shearing function.

In undertaking the present study, the writer has assumed, as a working hypothesis, that differences in lizard dentitions are adaptive, and that the selection that has produced them is exerted through the medium of diet. In accordance with this hypothesis, certain requirements must be met in order that results achieved by the study may be conclusive. First, obviously, differences in diet and dentition must be shown to exist within the group investigated. Second, it must be demonstrated that forms with similar diets have similar dentitions, and conversely, that forms with different diets have correspondingly different dentitions. Third, dietary differences, with their associated dentitional differences, must occur within taxonomic boundaries based upon other than dentitional characters, and dietary and dentitional similarities must transgress such taxonomic boundaries.

It is the consensus among herpetologists that most lizards will eat anything they can overpower and swallow. To some extent this is true, but it is shown that consistent differences do exist between the diets of different forms. For example, there are clear-cut differences between the diets of *Sauromalus*, *Crotaphytus*, and *Phrynosoma*; in addition, more subtle differences, such as those between the diets of *Sceloporus g. graciosus* and *Uta s. stansburiana*, also appear to be consistent. Whether these differences reflect different relative abundance of various food materials in different environments, or different intrinsic "preferences" among the lizards, is immaterial to the present discussion. The point is that such differences exist.

Determination of differences among dentitions is difficult because of the high variation of each dentition character within a single taxonomic group. The greater part of this variation is due to inaccuracy, which results from the small size of the material. A lesser part is intrinsic variation caused by the manner of tooth replacement found in reptiles.

No dentition group can be shown to be a discrete entity by statistical methods, but such fine distinction cannot be expected. Morphologically, the lizards of the series under discussion make up a fairly close-knit section of the family Iguanidae (Camp, 1923). This relationship implies a certain community of genetic substrate, which may be used for assuming similarity of dentition, since dental characters were not used in the original determination. With this concept as a background, the dentition groups described in the present study are intended to represent extremes, toward which dentitions of taxonomic groups exhibit varying tendencies.

Close agreement between dentition and diet is found in *Phrynosoma platyrhinos*, *P. douglassii ornatissimum*, and *P. cornutum*; diet and dentition of *Crotaphytus c. collaris* and *C. c. baileyi* are also similar. Between *Phrynosoma*

and *Crotaphytus* there is a great deal of difference in both diet and dentition; no species of either genus approaches conditions found in the other genus with respect to diet or dentition. Except for being within the frame of the series under discussion, *Phrynosoma* and *Crotaphytus* are not closely related, and it is difficult to judge how much of the dentitional divergence between the two is due to adaptation to divergent diets, and how much is associated with divergent characters adapted to environmental factors other than diet.

In the three species of *Sceloporus* studied, dentitions are generally similar and diets are rather varied. The diet of *S. m. magister* resembles that of *Phrynosoma* most closely of the three, and the diet of *S. g. graciosus* resembles that of *Crotaphytus* most closely, the diet of *S. undulatus* being approximately intermediate in the dietary range of the genus. The dentition of *magister* shows pronounced tendencies toward the *Phrynosoma* condition, while the dentition of *graciosus* shows equally pronounced tendencies toward the condition of *Crotaphytus*. Like diet, dentition of *undulatus* is approximately intermediate. *Sceloporus* is not much more closely related to *Phrynosoma* than to *Crotaphytus*. Mittleman (1942) and Smith (1946) place all three in separate sections of the North American Iguanidae. Divergence of dentitions among the species of *Sceloporus* tends toward conditions found in genera whose relations to *Sceloporus* itself are approximately equally distant; divergence of diets corresponds closely to that of dentitions. The general similarity among the dentitions of *Sceloporus* is a reflection of the common genetic background of the genus; divergence from the common pattern appears to be controlled by adaptation to divergent diets.

Dentitions of *Callisaurus draconoides ventralis* and *Urosaurus ornatus levis* are very similar, and are distinct from other dentitions in the present series. Diets show a corresponding similarity to each other and distinctness from other diets in the series. *Callisaurus* is very closely related to *Holbrookia*, and *Urosaurus* is considered a recent derivative of *Sceloporus*. With respect to both diet and dentition, *Callisaurus* and *Urosaurus* are much more similar to each other than either is to its nearest relative. This relationship is interpreted as a rather striking case of convergence, with diet playing an important role in selection.

Dentitions of *Dipsosaurus d. dorsalis, Sauromalus obesus,* and *Ctenosaura similis* are similar to each other, and as a group are highly distinctive. Diets are also similar and highly distinctive. The three genera are assigned to the same section of the Iguanidae by Mittleman, and they are probably closely related. Assuming that this supposition is correct, alternative interpretations may be made. One is that they have retained ancestral diet, and consequently ancestral dentition, while evolving to their present level of generic distinction. The alternative interpretation is that early in their history the ancestors of all three genera acquired similar food habits; as a result, dentitions evolved in a parallel manner, while selective factors acting on non-dentitional characters wrought the changes that produced the present three genera. Although it is not generally accepted, the possibility that *Dipsosaurus, Sauromalus,* and *Ctenosaura* are similar because of convergence cannot be eliminated. Unlike the other sections under discussion, this one is established partly on the basis of dentitional characters. If the members of this section have attained their sim-

ilarity through convergent evolution, it is probable that the selective effect of diet has played a part in the process.

The dentition of *Uta s. stansburiana* resembles that of *Crotaphytus* in about half of its characters, and that of *Callisaurus* and *Urosaurus* in the other half. The characters in which *Uta* resembles *Crotaphytus*, i.e., degree of cuspation, position of first cuspate tooth, and profile, appear to be more highly developed in *Uta*. Sharpness of teeth of *Uta*, in which it resembles *Callisaurus* and *Urosaurus*, could also be interpreted as a higher development of the condition met with in *Crotaphytus*. Diet of *Uta* is distinctive in containing a large percentage of food animals of intermediary activity; if these forms have the same relation to *Uta*, on account of its smaller size, that active forms do to a large lizard like *Crotaphytus*, the diet of *Uta* then bears a very considerable similarity to that of *Crotaphytus*.

Dentition of *Gambelia wislizenii* is similar in most respects to that of *Uta*, with a slightly greater resemblance to the dentition of *Crotaphytus* than that shown by *Uta*. Diet of *Gambelia* is essentially similar to that of *Crotaphytus*, although a greater component of vertebrates in the diet of the former suggests that it tends to prey upon more active forms than does the latter. Phylogenetically, *Gambelia* and *Crotophytus* are very closely related; the observed differences between the dentitions of the two forms may be due to this tendency of the diets to diverge. *Uta*, on the other hand, is very closely related to *Sceloporus*; the resemblance of its dentition to that of *Gambelia* and *Crotaphytus* can be interpreted as an example of convergence through dietary similarity.

In general, dentition of *Holbrookia texana* resembles that of *Crotaphytus*, *Callisaurus*, and *Urosaurus* about equally, with a slight similarity to that of *Sceloporus undulatus elongatus*. Diet resembles that of *Crotaphytus* and *Callisaurus* and *Urosaurus* more than it does that of *S. undulatus*. With diet and dentition as undistinctive as they are in *Holbrookia*, a clear-cut interpretation is impossible. As has been mentioned, *Holbrookia* is most closely related to *Callisaurus*, and slightly more distantly to *Crotaphytus*; since both dietary and dentitional resemblances tend almost entirely toward these closely related forms, the relationship contributes little to the discussion.

To recapitulate briefly, it appears that there are four adaptive types of dentition present in the series of North American Iguanidae studied. These types are:

Herbivorous: Teeth with strong lateral compression, highly cuspate, sharp, and blade-like. Crown line even; profile variable, apparently unimportant. Associated with diet of vegetable material. Exhibited by *Dipsosaurus d. dorsalis, Sauromalus obesus,* and *Ctenosaura similis.*

Ant-eating: Teeth blunt, stout, and peglike, essentially non-cuspate. Crown line uneven; profile obscure, unimportant. Associated with diet greatly predominant in ants. Exhibited by *Phrynosoma platyrhinos, P. douglassii ornatissimum,* and *P. cornutum.*

Predaceous (type A): Teeth sharp, slender and rather cylindrical except at apex; cuspation poor to moderate. Crown line even; back teeth essentially as high as front. Associated with diet predominant in active forms, in particular those with heavy integument. Exhibited by *Callisaurus draconoides ventralis* and *Urosaurus ornatus levis.*

Predaceous (type B): Teeth moderately sharp, stoutly conical, moderately to highly cuspate. Crown line even; profile apparently important, front teeth tend to be abruptly higher than back teeth. Associated with diet predominant in very active forms, in particular those with integument of intermediate weight. Exhibited by *Crotaphytus c. collaris,*

C. c. baileyi, Gambelia wislizenii, and *Uta s. stansburiana. Gambelia* and *Uta* exhibit the characters of predaceous type B to the highest degree, i.e., teeth are sharper, slenderer, and more highly cuspate, and in *Uta* the characteristic profile is more highly developed. *Sceloporus g. graciosus* probably belongs to predaceous type B also, but *S. undulatus elongatus* and *S. m. magister* represent gradations between it and the ant-eating type of dentition. *Holbrookia* is possibly an intermediate between predaceous types A and B, but evidence in its case is inconclusive.

It is not known how many more such adaptive types of dentition may exist among the North American Iguanidae. Presumably there are few, since this survey has covered representatives of nearly all the taxonomic sections of the group. However, it has been largely restricted to forms from semi-arid and arid regions, and it is possible that more adaptive types may appear among lizards from moister regions, perhaps among the genus *Sceloporus,* for example. There is little indication of the number of additional types to be found in other sections of the Iguanidae; it would be interesting to investigate tropical species of the Iguanidae along these lines. There is also little indication of the number of possible dentition types to be found among other families of lizards. The South American teiids would make excellent subjects for such a study, if enough data on diet could be gathered; the most fruitful line of attack might be a comparison of *Tupinambis* and related forms with *Dracaena* and related forms. The dentition of *Tupinambis* is characterized by having anterior teeth which are extremely high-crowned, conical, sharp, and recurved, and posterior teeth which are low-crowned and cuspate. The anterior teeth of *Dracaena,* on the other hand, are relatively low-crowned and conical, while the posterior teeth are great, flat, oval "crushers," rather on the order of the back teeth of mature specimens of *Varanus niloticus,* but flatter. The most immediate obstacle to the prosecution of these studies is the lack of adequate data concerning diet.

SUMMARY

Differences among diets of lizards in a series of North American Iguanidae are shown to exist; these differences are probably consistent.

Similarly consistent differences are discernible among dentition of the series studied.

Dietary and dentitional differences correspond; that is, forms with similar dentitions have generally similar diets, and forms with different diets have different dentitions.

On the hypothesis that differences observed in dentitions are the result of selection operating through the medium of diet, possible selective effects of a number of different dietary components are discussed.

In some cases, closely related forms have different dentitions, indicating divergent evolution with respect to dentition; in other cases, distantly related forms have similar dentitions, indicating evolutionary convergence with respect to dentition.

Four dentition types, which appear to be adaptive to minor dietary specializations, are defined among the series of Iguanidae studied. Intergrades between some of these are pointed out.

Several lines of future inquiry are pointed out, including investigation of diet and dentition in other parts of the family Iguanidae, and in other families of lizards.

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Notes on Mississippi Amphibians and Reptiles*

Philip W. Smith and James C. List

*Illinois Natural History Survey and Department of Zoology,
University of Illinois, Urbana*

During most of July and August of 1951, while attending the summer session at the Gulf Coast Research Laboratory near Ocean Springs, Mississippi, approximately 800 specimens of amphibians and reptiles were secured in the "panhandle" counties of southern Mississippi, on some of the offshore islands, and in short stops while en route to and from Ocean Springs. This material is deposited in the University of Illinois Museum of Natural History, the Illinois Natural History Survey collection, and in the private collection of the junior author. A second collection of approximately 200 specimens largely from the Delta region, deposited in the Delta State Teachers College Museum, has been made available to us through the courtesy of Dr. R. L. Caylor of that institution. These two collections contain 89 species and subspecies as follows: salamanders, 14; frogs and toads, 19; lizards, 8; snakes, 36; and turtles, 12.

Inasmuch as the snakes and lizards of Mississippi have been treated by Miss Cook (1943a, b) and three shorter papers on the herpetofauna of the Gulf counties have appeared (Brimley, 1910; Corrington, 1927; and Allen, 1932), only county records or specimens of special interest for other reasons are cited in the present paper. Thus the following list is not a complete list of species and specimens collected since the bulk of our material is from Harrison County, the county best known. Despite the several papers cited above, Mississippi remains one of the least known states herpetologically, and it is felt that the distributional records and other notes accumulated for the following 76 forms merit publication.

SALAMANDERS

Amphiuma means (Garden).—One specimen was captured in a roadside, weed choked pool four miles north of Ocean Springs, Jackson County. This specimen, 751 mm in total length, has two toes per foot and 62 costal grooves. The dorsum and venter are an almost uniform blue-black.

Amphiuma tridactylum Cuvier.—A small specimen from Jones Bayou near Cleveland

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* Contribution from the Gulf Coast Research Laboratory, Ocean Springs, Mississippi.

and a juvenile from Benoit, both in Bolivar County, are present in the Delta State Teachers College collection.

Diemictylus viridescens louisianensis (Wolterstorff).—Two small efts were taken under logs in a wet prairie one and one-half miles south of Hurley, Jackson County. A specimen from Legion Lake near Rosedale, Bolivar County, is present in the Delta State Museum.

Ambystoma opacum (Gravenhorst).—The laboratory at Delta State contains specimens of this species from Beulah, Bolivar County; Leaf River, Forrest County; and Marks, Quitman County.

Ambystoma texanum (Matthes).—One specimen from Charleston, Tallahatchie County, is present in the collection at Delta State Teachers College.

Plethodon glutinosus (Green).—Fifteen specimens taken six and one-half miles northeast of Vancleave and one specimen from one and one-half miles east of Ocean Springs, Jackson County, cannot be allocated with certainty to subspecies. The costal grooves range from 13 to 15 (14 in 77%) and the dorsal flecks are much reduced in size and barely perceptible in preserved specimens but were neither metallic nor gold in life. The largest specimen is 56 mm from snout to vent and the average snout-vent length of the eight largest specimens is 51 mm. Costal folds between the adpressed limbs of adults range from one to three; in juveniles the adpressed limbs touch or overlap. The lateral spots are lichen-like but smaller and less pronounced than in comparative material from the north. Two small specimens had a metallic silver sheen on the sides in life.

The Delta State collection contains specimens of this species from Jackson, Hinds County; Marks, Quitman County; Charleston, Tallahatchie County; New Albany, Union County; and Eupora, Webster County.

Eurycea bislineata cirrigera (Green).—Five specimens from six miles northeast of Vancleave and one specimen from five and one-half miles north of Escatawpa, both in Jackson County, were secured.

Eurycea longicauda guttolineata (Holbrook).—Eleven specimens of this common salamander were taken six miles northeast of Vancleave, Jackson County. Specimens from Ocean Springs, Jackson County; Stewart, Montgomery County; and New Albany, Union County, are deposited in the Delta State collection.

Desmognathus fuscus brimleyorum Stejneger.—A series of 30 specimens from a magnolia forest six miles northeast of Vancleave, Jackson County, is referable to this subspecies although this locality falls within the range of *D. f. auriculatus* as recently defined by Grobman (1950, figs. 1-2). Five of the 30 are dark gray, tan, or brown with the ventrolateral and dorsolateral rows of light spots present somewhere on the tail and body and with dark pigment predominating on the venter. These five approach typical *auriculatus* taken in southern Harrison County. Ten of the 30 are more or less uniformly mottled ventrally with light and dark flecks subequal in extent. Twelve of the 30 have light venters with scattered patches of pigment. Dorsal pattern and color of the latter two groups are variable.

This sample indicates that the range of *D. f. auriculatus* is apparently restricted to an even narrower belt along the coast in Mississippi than shown by Grobman's figures (*ibid.*) and that inland from the seacoast in southeastern Mississippi at least, intergradation of *auriculatus*, *brimleyorum*, and *fuscus* occurs.

The Delta State collection contains two specimens from Stewart, Montgomery County and one from Hattiesburg, Forrest County.

Manculus quadridigitatus (Holbrook).—Six specimens were taken in a magnolia forest six miles northeast of Vancleave and seven, from a cypress swamp five and one-half miles north of Escatawpa, Jackson County. Snout-vent lengths range from 23 to 33.2, averaging 26.2 mm. The number of costal grooves ranges from 15 to 17, averaging 16. Costal folds between the adpressed limbs range from three to seven, averaging 4.8.

Pseudotriton ruber vioscai Bishop.—One specimen was found in a seep in a magnolia forest six miles northeast of Vancleave, Jackson County. This specimen, 162 mm in total length, is dark orange-brown with large dark brown dorsal spots, many of which are fused, and much smaller brown flecks over the sides and venter. Vomerine series are right angled

and the posterior processes are not closely approximated. There are 16 costal grooves and six and one-half folds between the adpressed limbs.

The Delta State Museum contains another adult specimen from Hattiesburg, Forrest County, and two larvae from Stewart, Montgomery County.

SALIENTIANS

Bufo woodhousii fowleri (Hinckley).—Twelve specimens were secured as follows: one, one mile north of Arkabutla Reservoir, De Soto County; eight, six miles northeast of Vancleave and two, five and one-half miles north of Escatawpa, Jackson County; and one, three miles south of Canton, Madison County. The collections at Delta State contain in addition specimens from Boyle and Cleveland, Bolivar County; Stewart, Montgomery County; Maben, Oktibbeha County; Charleston, Tallahatchie County; Ripley, Tippah County; and New Albany, Union County.

Although *B. terrestris* was abundant in the coastal meadows and on some of the offshore islands, no specimens of *fowleri* were seen or heard in the coastal area during our stay.

Bufo terrestris terrestris (Bonnaterre).—Fifty-six specimens were collected as follows: six, one and one-half miles east of Ocean Springs; eight, Ocean Springs; six, four miles north of Ocean Springs; three, three miles north of Ocean Springs; three, three miles northeast of Ocean Springs; one, one and one-half miles south of Hurley; one, three miles south of Hurley; one, five and one-half miles north of Escatawpa, all in Jackson County; one, three miles north of Vestry, George County; one, twelve and one-half miles north of Cybur, Pearl River County; ten, Horn Island, and fifteen, Cat Island, Mississippi Sound.

Several specimens in the lot are separable from *B. w. fowleri* only by the posteriorly knobbed parietal crests. Confusion of these species is precluded, however, inasmuch as the crests are distinctly knobbed in specimens as small as 30 to 35 mm from snout to vent. Of special interest are two of the specimens from Cat Island which measure, respectively, 97 and 94 mm from snout to vent. Another DOR specimen equally large was seen but not saved. The largest mainland specimen is 77 mm from snout to vent. Allen (1932) mentions four such large examples from the same island. These giants appear to differ only in their larger size, heavier cranial crests, and perhaps by the rusty red color (in life).

Bufo quercicus Holbrook.—Twenty specimens were collected as follows: eight, three miles north of Vestry, George County; five, three miles south of Hurley; one, five miles north of Escatawpa, Jackson County; and six, five miles west of Ramsey Springs, Stone County. Evenings following rains oak toads appeared to be in every ditch and specimens could be heard singing continuously except for a narrow zone along the ocean.

The Mississippi specimens differ rather markedly from comparative material from peninsular Florida, possessing more strongly developed cranial crests, wartier skins, and larger parotoid glands. Eighty-two specimens available from Louisiana, Mississippi, Georgia, South Carolina, and northern Florida are similar in cranial crest development and wartiness. In 52% of these toads the greatest length of the parotoid gland, when projected forward, extends from the anterior edge of the parotoid to a point anterior to the eye. Forty-three specimens from peninsular Florida are uniform in the possession of smoother skin, lower crests, and in only 2% does the projected parotoid gland length extend anterior to the eye. Although the Florida toads are recognizably distinct, we feel the differences are too slight to warrant taxonomic recognition.

Acris gryllus gryllus (LeConte).—Sixteen specimens were secured; two from nine and one-half miles east of Lumberton, Forrest County; two, six and one-half miles north of Durant, Holmes County; eight, three miles south of Hurley and three, one and one-half miles south of Hurley, Jackson County; and one, six miles west of Vestry, Stone County. The museum at Delta State contains a number of *Acris* from the Delta region which we prefer not to allocate inasmuch as these specimens are not now at hand.

Pseudacris nigrita feriarum (Baird).—Seven specimens from three miles north of Vestry, George County, and seven from ten and one-half miles northwest of Biloxi, Harrison County, exhibit intergradation with *P. n. nigrita*. Two specimens have a weak dorsal pattern; the others possess linear series of spots suggesting stripes, but in most specimens

the spots are not rounded and closely approximated as in the typical subspecies. The body shape and leg bars, however, are typical of *P. n. nigrita*. The tibia/body ratios range from 48.2 to 53.4%, averaging 50.2%. Typical specimens of *P. n. feriarum* from Stewart, Montgomery County; New Albany, Union County; and Hollandale, Washington County, are present in the Delta State Museum.

Hyla cinerea (Schneider).—Twenty-nine specimens are present as follows: six, six and one-half miles north of Durant, Holmes County; eighteen, one and one-half miles east of Ocean Springs, Jackson County; and five, four and one-half miles south of Oakland, Yalobusha County. These series show a rather marked clinal variation in size. Several males from Holmes and Yalobusha counties are 60 mm from snout to vent whereas the largest breeding male from the coastal region is 52 mm and most are considerably smaller. One specimen from Harrison County was puzzling in life, possessing obscured dark spots in the olive ground color and an irregular light stripe on the left side. These features suggested *Hyla gratiosa* but proportions of the specimen are typical of *Hyla cinerea* and in preservative the dorsal dark spots have disappeared.

The Delta State collection contains specimens from Cleveland and Rosedale, Bolivar County; and one mile west of Lake Washington, Issaquena County.

Hyla femoralis Latreille.—Thirty-one specimens were collected as follows: one, three miles north of Vestry, George County; two, four miles north of Ocean Springs and four, one and one-half miles south of Hurley, Jackson County; three, two miles west of Ramsey Springs and 21, six miles west of Vestry, Stone County. After rains this species rivaled *B. quercicus* and *Hyla squirella* in abundance. During the day specimens were occasionally found under bark of stumps and within pitcher plants. One specimen is aberrant, possessing (in life) a suborbital light spot on the right side.

Hyla gratiosa LeConte.—Three specimens from four and one-half miles northeast of Ocean Springs; one from one and one-half miles south of Fontainebleau, Jackson County; and four from one and one-half miles north of the Jackson County line, George County, are in the collection. These frogs were heard on only a few occasions, usually following moderately hard rains. Clasping pairs were found on three occasions.

Hyla avivoca avivoca Viosca.—A series of five singing adults, ranging from 31 to 34 mm in snout-vent length, was secured in a swamp at the north edge of Orange Grove, Jackson County. The extreme reduction in dorsal pattern and slender body form displayed by these specimens prompted us to borrow material from various parts of the range for direct comparison. The reduced pattern of the Mississippi frogs was found, however, to be duplicated by occasional specimens from southern Illinois, Louisiana, Florida, and Georgia, although a large proportion of the borrowed material possesses *versicolor*-like dorsal blotches.

Hyla squirella Latreille.—New distributional records of this extremely abundant frog are one specimen from one and one-half miles east of Ocean Springs, Jackson County, and two from four miles south of Ramsey Springs, Stone County. On rainy nights hundreds of specimens could be seen in flooded fields, ditches, and small ponds, but specimens were found during the day only three times.

Hyla versicolor versicolor (LeConte).—Three specimens were taken two miles west of Ramsey Springs, Stone County. These specimens are markedly more tuberculate dorsally and have more yellow in the groin and concealed surfaces of the legs than do specimens from southern Illinois. The usually characteristic suborbital light spot is barely evident in one specimen, absent in the others.

Rana sevosa Goin and Netting.—One specimen was found July 15, under a log at the edge of a small cypress pond three miles south of Hurley, Jackson County. Although 36 of the 50 paratypes were collected in Jackson County, Mississippi, the present specimen is of note since it seems to be the first young specimen to be reported.

This frog, 31 mm from snout to vent, is obviously newly metamorphosed since a distinct tail stub is present and the tympani are invisible. The dorsolateral folds and post-tympanic folds are very broad but disappear at midbody. The dorsal skin is moderately smooth and the ground color dorsally is a light slate color with many disitnct dark spots which are not light margined. Lateral spots are lighter and less prominent. The legs are conspicuously marked with dark bands equal in width to the interspaces. The chin and

anterior and posterior surfaces of the thighs are lightly mottled with brown; the remainder of the venter is white.

This juvenile is referred with reluctance to this species inasmuch as in most diagnostic features it is more like *Rana capito* which it also resembles in general appearance. It is probable that immatures of these two species are indistinguishable, however, and Goin and Netting (1940) have shown that older literature records of *R. capito* in the Gulf area were actually based on specimens of *R. sevosa*.

A series of newly transformed *Rana areolata circulosa* from central Illinois is available for comparison. These differ from the single immature *R. sevosa* in having light margined dorsal spots; four or less dark bands across the tibia (five in *sevosa*); tibia length less than half the snout-vent length (about half in *sevosa*); distinct mottling on the upper jaw (a few maxillary flecks in *sevosa*); distinct tympani; and in size. Ten young *R. a. circulosa* of corresponding stage in development range from 22.2 to 24.2 mm, averaging 23.8 mm from snout to vent. The specimen of *R. sevosa* is 31 mm in snout-vent length. Adults of *R. sevosa*, however, average about 10 mm shorter than adults of *Rana areolata circulosa*.

Rana catesbeiana Shaw.—One female, 96 mm from snout to vent, from four and one-half miles south of Durant, Holmes County, and a male, 117 mm in snout-vent length, from Ocean Springs, Jackson County, were taken. The species was heard several times but at only one locality, a small artificial pond in Harrison County.

The Delta State collection contains specimens from Pace and Rosedale, Bolivar County and Stewart, Montgomery County.

Rana clamitans Latreille.—One specimen from four and one-half miles south of Durant, Holmes County, and nine from Jackson County (one, three miles north of Ocean Springs; four, Vancleave; one, six miles northeast of Vancleave; three, one and one-half miles east of Ocean Springs) are in the collection. The five adults are small, ranging from 50 to 58 mm in snout-vent length and averaging 53 mm. The specimen from Holmes County, a male 50 mm from snout to vent, has greatly shortened femora, the length barely exceeding the diameter of the thighs. The tibiotarsal articulation thus reaches only the middle of the enormously enlarged tympanum when the legs are carried alongside the body. This toad-like specimen is dark brown above with the upper surfaces of forelegs, tibiae, and feet conspicuously lighter and unmarked.

Rana grylio Stejneger.—Four specimens from four miles north of Ocean Springs, one from five and one-half miles northeast of Ocean Springs, and one from two and one-half miles south of Fontainebleau, all in Jackson County, are of this species. The distinctness of this species from *Rana catesbeiana* cannot be questioned after seeing *R. grylio* in life and hearing its call. On a few occasions both species were heard the same night but never together, *grylio* occurring only in brushy swamps. The postfemoral stripes, usually considered diagnostic, are present in only two of our specimens. *R. grylio* is nevertheless readily separated from *R. catesbeiana* by color and the following measureable characters: first and second fingers of the forelegs are equal or the second is longer in *grylio* whereas in *catesbeiana* the second finger is usually shorter than the first; the horizontal diameter of the tympanum is $\frac{3}{4}$ or more the inter-tympanic space in male *R. grylio*, usually less than $\frac{3}{4}$ in male *catesbeiana*; the head length-body ratio in male *grylio*, is 40% or more, less than 40% in male *catesbeiana*. Only one female *grylio* was secured.

Rana pipiens sphenocephala (Cope).—Specimens were taken as follows: one, seven and one-half miles east of Lumberton, Forrest County; one, three miles northeast of Vestry and one, eleven miles west of Vestry, George County; one, one and one-half miles east of Ocean Springs, Jackson County; and one, twelve and one-half miles south of Goodman, Madison County. The Delta State Museum contains specimens from Cleveland, Bolivar County; and Stewart, Montgomery County.

Microhyla carolinensis carolinensis (Holbrook).—Narrow mouthed toads were abundant in the coastal area and even light showers resulted in choruses of these frogs in ditches and puddles. Specimens were collected as follows: one, three miles south of Hurley and one, six miles northeast of Vancleave, Jackson County; one, twelve and one-half miles north of Cybur and one, seventeen and one-half miles north of Cybur, Pearl River County; and two, four miles south of Ramsey Springs, Stone County. The collection at

Delta State contain specimens from Ocean Springs, Jackson County, and Charleston, Tallahatchie County.

LIZARDS

Anolis carolinensis Voigt.—Three specimens from one and one-half miles east of Ocean Springs, Jackson County, and four from Cat Island were collected. Specimens from Charleston, Tallahatchie County, and Leroy Percy State Park, Washington County, are in the Delta State collection.

Sceloporus undulatus undulatus (Latreille).—Five specimens from Jackson County (one, one mile south of Hurley; two, four miles north of Ocean Springs; one, six miles northeast of Vancleave; and one, three miles north of Escatawpa) are in the collection. Dorsal scale row counts range from 33 to 38, averaging 35.6.

Cnemidophorus sexlineatus (Linnaeus).—A series of 16 specimens from Cat Island and single specimens from four miles north of Ocean Springs and two and one-half miles southwest of Fontainebleau, Jackson County, are new distributional records. The Delta State Museum contains specimens from Charleston, Tallahatchie County.

In all, six specimens are available from the mainland and six from Horn Island in addition to the Cat Island series. The mainland series vary in femoral pore counts from 14 to 15, averaging 14.4, and have one complete row of granules separating the supraoculars from the superciliaries. Femoral pore counts of the Horn Island series range from 14 to 16, averaging 14.7 per side, and also have a single complete row of granules separating supraoculars and superciliaries. Femoral pore series of the 16 Cat Island lizards range from 14 to 18, averaging 16.2 per side, and 15 of the 16 specimens have two complete rows of granules between supraoculars and superciliaries. Correlated with the increased number of granules the anterior and posteriormost supraoculars are reduced in size. In color, pattern and other scutellation features, however, the Cat Island specimens do not appear significantly different.

Scincella laterale (Say).—Additional records of this species are as follows: two, two and one-half miles east of Ocean Springs; one, four miles north of Ocean Springs; one, three miles northeast of Ocean Springs; three, six miles northeast of Vancleave, Jackson County; one, Horn Island, and two, Cat Island. A specimen from Charleston, Tallahatchie County, is present in the Delta State collections. These skinks were abundant on the outlying islands as well as on the mainland.

Eumeces fasciatus (Linnaeus).—Since Mississippi authors have not distinguished this species from the related *E. inexpectatus* and *E. laticeps*, it seems desirable to list all specimens of these species secured. This skink was found as follows: two, four miles south of Collins, Covington County; six, six miles north of Biloxi, Harrison County; one, six miles northeast of Vancleave, Jackson County; and one, twelve and one-half miles north of Cybur, Pearl River County. The Delta State Museum contains specimens from five miles west of Cleveland, Bolivar County; Ocean Springs, Jackson County; and Marks, Quitman County.

In ten specimens at hand the number of scale rows at midbody is 28 to 30. One specimen has a supralabial formula of 7-8; the others, 7-7. The median row of subcaudals is distinctly widened and two subequal postlabials are present in all ten specimens.

Eumeces inexpectatus Taylor.—One specimen from Cat Island, one from Ramsey Springs, Stone County, and fifteen from Jackson County (one, two and one-half miles north of Ocean Springs; one, four miles north of Ocean Springs; three, three miles northeast of Ocean Springs; three, one and one-half miles north of Ocean Springs; one, three miles south of Hurley; one, four and one-half miles north of Fontainebleau; one, one and one-half miles east of Ocean Springs) were taken. A clutch of eleven eggs was discovered August 11, under the bark of a rotten log. The nest was revisited August 14, apparently the day of hatching since several of the young remained in the nest site. Only four of them were secured. These hatchlings with red head stripes differed markedly from juvenal *fasciatus* and *laticeps*.

Eumeces laticeps (Schneider).—The Delta State Teachers College collection contains examples of this species from five miles west of Cleveland, Bolivar County.

Eumeces anthracinus pluvialis Cope.—Three specimens of this rare lizard were secured as follows: one, nine and one-half miles east of Lumberton, Forrest County; one, eight

and one-half miles northwest of Biloxi, Harrison County; and one, one and one-half miles south of Hurley, Jackson County. All three specimens have 7-7 supralabials, the posterior three of which are light centered in each specimen. The number of scale rows at midbody is, respectively, 28, 27, and 26. The Forrest County specimen, a large male, has a more or less distinct middorsal light stripe.

SNAKES

Carphophis amoena helenae (Kennicott).—One female, 210 mm in length, was taken 16 miles north of Vancleave, Jackson County. This specimen has 13 dorsal scale rows, 134 ventrals, 27 caudals, 6-6 supra- and infralabials, 1-1 temporals and fused prefrontals and internasals. The Delta State collection contains specimens from Charleston, Tallahatchie County, and Yazoo County.

Farancia abacura reinwardtii Schlegel.—A half grown specimen was found DOR seven and one-half miles south of Collins, Covington County. The Delta State collection has specimens from Rosedale and Cleveland, Bolivar County, and Stewart, Montgomery County.

Diadophis punctatus stictogenys Cope.—Three adults were collected under boards and logs in Jackson County as follows: one, thirteen and one-half miles south of Hurley, one, three miles northeast of Ocean Springs, and one, ten miles northeast of Ocean Springs. A clutch of three eggs was found under bark of a rotten log one and one-half miles north of Ocean Springs on July 12. At room temperature all three eggs hatched July 29, the young measuring 98, 102, and 103 mm in length. Ventrals in the six adult specimens range from 135 to 145, averaging 140. Upper labials are seven in each case.

Specimens from Charleston, Tallahatchie County, and Ripley, Tippah County, are present in the Delta State collection.

Heterodon platyrhinos platyrhinos Latreille.—A large specimen of this snake taken one and one-half miles east of Ocean Springs, Jackson County, managed to escape before it could be preserved. This fine example had a ground color of very light sand color with unusually distinct dorsal and lateral blotches. The Delta State collection has a specimen from Ripley, Tippah County.

Opheodrys aestivus (Linnaeus).—Nine specimens were collected in the shrubbery around a pond one ond one-half miles east of Ocean Springs and one specimen was found DOR three miles northeast of Ocean Springs, Jackson County. Most of the living snakes were found at night by searching the shrubbery with a gasoline lantern. All ten snakes have 17-17-15 scale rows, 7-7 supralabials, and 8-8 infralabials. Ventral counts in males range from 156-160; in females, 145-162. Subcaudal counts in males range from 146-147; in females, 130-139. Total lengths range from 199 to 768 mm.

Specimens in the Delta State collection are from Merigold and Beulah, Bolivar County, and New Albany, Union County.

Coluber constrictor priapus Dunn & Wood.—Seven specimens are in the collection as follows: one, Deer Island, Mississippi Sound; one, four miles south of Collins, Covington County; one, two miles south of Fontainebleau; one, four miles north of Fontainebleau; two, one and one-half miles south of Hurley; and one, one and one-half miles east of Ocean Springs, Jackson County. The six females exhibit the following variation: ventrals 172-182, averaging 177; subcaudals 86-97, averaging 91; supralabials 7-7 to 8-8; infralabials 9-9 to 8-10. The single male has 173 ventrals, 72+ subcaudals, 8-8 supralabials, and 9-10 infralabials. Total lengths range from 751 to 1352 mm. These very common snakes are known locally as black runners.

The Delta State collection contains racers from Pace, Bolivar County, and Leroy Percy State Park, Washington County. In color these snakes from west central Mississippi are quite distinct from the coastal specimens. The Delta racers are lighter above and below without the very prominent white throat of typical *priapus.* Scutellation data for these two snakes are not now available.

Elaphe guttata guttata (Linnaeus).—One young specimen, taken one and one-half miles east of Ocean Springs, has 23-27-19 scale rows, 217 ventrals, 70 subcaudals, 8-8 supralabials, 12-13 infralabials, and a total length of 388 mm. There are 32 body blotches and 13 tail spots. The Delta State collection contains a large specimen from Eupora, Webster County.

Elaphe obsoleta confinis (Baird & Girard).—A juvenile from two miles south of D'Lo, Simpson County, and a somewhat larger specimen from six and one-half miles northeast of Vancleave, Jackson County, are in the collection. Scutellation data for these males are, respectively: scale rows 25-27-19, 25-26-19; ventrals 241, 242; subcaudals 88, 85; supralabials 8-8; infralabials 11-11; total length 560, 858 mm; tail length 102, 159 mm; body blotches 29; tail spots 12. A specimen from Amite County is present at Delta State.

Rhadinaea flavilata (Cope).—The Delta State collection contains a specimen from Ocean Springs, Jackson County. Three specimens taken in piles of driftwood on a floodplain six miles north of Biloxi, Harrison County, are not county records, but standard data for these rare little snakes may be of interest: scale rows, 17 in all; ventrals 133, 132, 133; subcaudals 66, 71, 17+; supralabials 7-7; infralabials 9-9; and temporals 1-2. Total lengths range from 265 to 295 mm.

Lampropeltis calligaster rhombomaculata (Holbrook).—A single juvenile, 450 mm in length, was found DOR at Vancleave, Jackson County. This specimen appears to be typical with 23-21-19 scale rows and distinctly red colored blotches. The head scales are too damaged to interpret.

Lampropeltis doliata doliata (Linnaeus).—One male, 450 mm in length, was found under bark of a fallen log six miles west of Vestry, Stone County. There are 17-17-15 scale rows, 178 ventrals, 45 subcaudals, 7-7 supralabials, 8-8 infralabials, and 1-2 temporals.

Lampropeltis getulus holbrooki Stejneger.—A specimen 1430 mm in length, still alive at present, from six and one-half miles northeast of Vancleave, Jackson County, is typical in pattern. Another specimen, 470 mm in total length, from one and one-half miles east of Ocean Springs, Jackson County, possesses light centered scales in a definite pattern of cross bands. Only an occasional scale between these bands has a white spot.

Natrix grahamii (Baird & Girard).—A specimen from Glen Allan, Washington County, and another from Pace, Bolivar County, are in the Delta State collection. The latter specimen, now at hand, yields the following data: male, 20-19-17 scale rows, 177 ventrals, 61 caudals, 7-7 supralabials, 10-10 infralabials, 1-2 and 1-3 temporals, 789 mm in total length, 137 mm in tail length.

Natrix cyclopion cyclopion (Dumeril & Bibron).—One young specimen still bearing an evident umbilical stalk but measuring 294 mm in total length was collected one and one-half miles east of Ocean Springs, Jackson County. This female has 27-29-21 scale rows, 139 ventrals, 69 subcaudals, 8-8 supralabials, 12-12 infralabials, 1-1 temporals, and a tail length of 73 mm.

Natrix rhombifera rhombifera (Hallowell).—One male was secured five and one-half miles north of Fontainebleau, Jackson County. This specimen has 27-27-21 scale rows, 142 ventrals, 80 subcaudals, 8-8 supralabials, 11-11 infralabials, 1-2 temporals, a total length of 966 mm and a tail length of 250 mm. The Delta State collection contains specimens from Rosedale, Cleveland, and Legion Lake, all in Bolivar County.

Natrix sipedon fasciata (Linnaeus).—Four specimens of this species, the most abundant water snake in the Biloxi region, are from Moss Point, two miles southwest of Fontainebleau, three miles north of Escatawpa, and six and one-half miles northeast of Vancleave, all in Jackson County. All four are females with 23-23-17 scale rows and eight supralabials. Ventrals range from 131-132; subcaudals, 64-69; infralabials, 10-11; temporals, 1-2 to 1-3; body blotches, 24-26; total lengths, 341 to 795 mm. Numerous other specimens were seen in fresh water, some within a mile or so of the brackish water habitats of *N. s. clarkii.* No evidence of intergradation between these two subspecies was noted.

Natrix sipedon clarkii (Baird & Girard).—The striped water snake was common in the brackish marshes and ponds on Deer Island, Mississippi Sound, where five adults ranging from 518 to 706 mm in total length were taken. Three of these gave birth to broods of four, eight, and eleven (plus two undeveloped eggs) young in the laboratory. The young varied from 180 mm to 230 mm in total length, averaging 211 mm. One of the young, which died shortly after birth, is an unusual duplication anomaly—a single head with two bodies, and is described more fully elsewhere (List and Smith, 1954).

In two of the 28 available specimens the lateral dark stripes are broken into linear series of blotches, at least posteriorly. In three others the lateral stripes approach this con-

dition, being constricted at intervals by vertical extensions of the upper adjacent light stripe. There is a tendency for the ventral stripes to break up into blotches in these snakes. Scale rows vary from 21-19-17 to 21-23-17, usually 21-21-19; ventrals range from 127-138, averaging 131; subcaudals range from 66-77, averaging 71; supralabials range from 8-8 to 9-9, usually 8-8; infralabials range from 9-9 to 11-11, usually 10-10.

Storeria occipitomaculata occipitomaculata (Storer).—The Delta State collection contains a specimen of this snake from Charleston, Tallahatchie County.

Haldea valeriae elegans (Kennicott).—Specimens are present in the Delta State collection from Ocean Springs, Jackson County; Charleston, Tallahatchie County; and Webster County. One female in a series of eight secured by us six miles north of Biloxi, Harrison County, is anomalous in possessing 5-5 supralabials (as in *H. striatula*), but is otherwise normal (17 scale rows, 113 ventrals, 41 subcaudals, 2 internasals, and weak keels).

Haldea striatula (Linnaeus).—Specimens from Ocean Springs, Jackson County, and Pace, Bolivar County, are present in the Delta State collection.

Thamnophis ordinatus ordinatus (Linnaeus).—A male taken two and one-half miles northeast of Ocean Springs, Jackson County, has 19-19-17 scale rows, 150 ventrals, 33+ subcaudals, 7-7 supralabials, 10-10 infralabials, a total length of 443+ mm, and a tail length of 62+ mm. This specimen is prominently checkered above, the inner row of black spots encroaching on the middorsal light stripe. The Delta State collection contains a specimen from Merigold, Bolivar County.

Thamnophis sirtalis sirtalis (Linnaeus).—Seven specimens from Jackson County were collected as follows: one, four miles north of Ocean Springs; three, one and one-half miles east of Ocean Springs; one, five miles north of Escatawpa; one, three miles north of Escatawpa; and one, four miles south of Fontainebleau. All seven snakes have 19-17 scale rows and three distinct light stripes on a brown background. Ventrals range from 149-161; subcaudals, 100-120. Five snakes have a 7-7 supralabials; one, 7-8; and one, 8-8. Five snakes have 10-10 infralabials; one, 9-9; and one, 8-8. None of the series has the parietal spots and contrasting pattern characteristic of *T. s. proximus*, whose occurrence has been reported for the Biloxi area.

Tantilla coronata coronata Baird & Girard.—A single female was taken in roots of a palmetto in Magnolia State Park, Jackson County. This specimen has 15 scale rows, 138 ventrals, 43 subcaudals, 7-7 supralabials, 6-6 infralabials, a total length of 188 mm, and a tail length of 36 mm.

Agkistrodon contortrix contortrix (Linnaeus).—Two adult males secured six and one-half miles northeast of Vancleave, Jackson County, provide the first record of the copperhead in coastal Mississippi. It is perhaps of interest that these specimens were taken in a deciduous woods of an unusually mesophytic nature for that region of pine meadows. These snakes have average band widths dorsally of 2.06 to 3.04 scale lengths; both specimens resemble eastern *mokeson* in color. Scale rows are 25-23-19; ventrals, 151, 154; subcaudals, 48 with four divided, 45 with 16 divided; body bands, 15, 12; tail rings, 5, 6.

The Delta State collection contains a specimen one meter in length from two miles north of Shaw, Bolivar County.

Agkistrodon piscivorus leucostoma (Troost).—Many more moccasions were seen in the Biloxi area than any other species of snake. Thirteen specimens are present from Horn Island and Cat Island, Mississippi Sound; five and one half-miles north of, five and one-half miles northeast of, and at Ocean Springs, Hurley, three miles south of Hurley, and five miles north of Escatawpa, all in Jackson County. Three specimens from Cat Island are much darker ventrally than any of our mainland snakes but no other differences are apparent.

These very abundant snakes appeared surprisingly docile in the gulf region, displaying none of the pugnacity of more northern cottonmouths. Most examples took flight and even when captured failed to exhibit the characteristic threatening behavior. Several snakes appeared much emaciated. One such specimen disgorged a smaller decapitated moccasin which had been killed the day before by boys.

Sistrurus miliarius barbouri Gloyd.—A single specimen found DOR one and one-half miles south of Vancleave, Jackson County, is referable to this subspecies. This snake, 300

mm in length, has 23-21-19 scale rows, 128 ventrals, subspherical and smooth edged dorsal blotches, and lateral spots in two rows. The ground color above is profusely pigmented with dark. Influence of the western race, *streckeri*, is seen in the number of anterior scale rows.

Sistrurus miliarius streckeri Gloyd.—Four specimens of this subspecies were captured in a single morning on Cat Island, Mississippi Sound, where the scrubby live oaks and Caribbean pines on sand hills evidently provide excellent habitat. One female gave birth August 10, to six young, ranging from 132 to 153 mm in length. One of these kept alive for six months fed on small lizards and frogs and at the time of death measured 173 mm in length.

All ten specimens are typical in color and pattern; eight of the nine now available have 23 anterior scale rows. One young has 24 anterior scale rows. Ventrals range from 124 to 130. The largest specimen taken is 440 mm in total length.

Crotalus horridus atricaudatus Latreille.—The Delta State collection contains a specimen from Yazoo County.

TURTLES

Sternotherus odoratus (Latreille).—The Delta collection contains specimens of this turtle from Lake Washington, Washington County, and Rosedale, Bolivar County.

Kinosternon subrubrum subrubrum X hippocrepis.—Four specimens (one, six miles south of Collins, Covington County; two, four miles north of Ocean Springs; one, three miles northeast of Ocean Spring, Jackson County) are intergrades. Three of these have numerous large yellow spots scattered over the top and sides of the head, one specimen has the head liberally spotted but fusion of some spots suggests the stripes of *hippocrepis*.

This species is exceedingly common in the coast region, occurring in ditches, marshes, temporary pools, and on one occasion in a water filled automobile track. The Delta State collection contains specimens from Charleston, Tallahatchie County; Hattiesburg, Forrest County; and Rosedale, Bolivar County.

Terrapene carolina subspecies.—The Delta State collection contains a specimen from Riley, Tippah County, which was tentatively identified as *T. c. carolina*. The expected race in northwestern Mississippi is *triunguis*, however, and the specimen is not now available for subspecific determination.

Terrapene carolina major (Agassiz).—Specimens of this turtle were secured as follows: one, seven miles north of Wiggins, Forrest County; four, two miles east of, and one, one mile northwest of Ocean Springs; and one, thirteen and one-half miles south of Hurley, Jackson County. This species was extremely common in the coastal region.

The largest specimen saved has a carapace length of 165 mm, but still larger specimens were encountered on a few occasions. One specimen was discovered laying four eggs near the laboratory at about 7 o'clock in the morning. Another large female was observed covering a clutch of two eggs at about 10 o'clock at night. In both cases the soil was rather dry and showed no evidence of having been moistened by the turtles.

Malaclemys terrapin pileata (Wied).—Eleven specimens were taken on Deer Island and one was found one mile east of Ocean Springs, Jackson County, on the mainland. Many of these turtles were collected in the mud and marshes of Deer Island and later released. A very large female found on the ocean side of the island had apparently just crawled up out of the ocean. Several examples were found with one or more legs mutilated, presumably by alligators which were reportedly common on Deer Island.

Two of the twelve specimens at hand have the sides of the carapace parallel; in the remaining specimens the shell is distinctly wider posteriorly. Three specimens are brown above, the rest black. One half grown specimen has a light colored head, each of the other eleven has a prominent black wedge-shaped mark on the top of the head.

Graptemys pseudogeographica kohnii (Baur).—Specimens are present in the Delta State collection from Rosedale, Bolivar County, and Lake Washington, Washington County.

Pseudemys floridana mobiliensis (Holbrook).—A large male found in a shallow ditch nine and one-half miles northwest of Biloxi, Harrison County, is puzzling. This specimen, 206 mm in carapace length and 80 mm in greatest height, has an immaculate yellow plas-

tron. The head pattern is also atypical, consisting of three longitudinal greenish-yellow stripes on the chin which are connected by a broad transverse band just anterior to the angle of the jaws. The outer stripes continue posteriorly, soon fusing with the suborbital stripes. The head pattern from above is typical. The carapace is remarkably similar to that of the common slider, *P. s. elegans.*

Pseudemys floridana hieroglyphica (Holbrook).—A juvenile, 85 mm in carapace length, from Pace, Bolivar ⌐⸱ ⸱nty, is present in the Delta State collection.

Pseudemys scripta elegans (Wied).—Common sliders were secured as follows: one, Moss Point, Jackson County; one, fourteen miles north of Cybur, Pearl River County; and one, four and one-half miles south of Oakland, Yalobusha County. The Delta State collection contains specimens from Cleveland and Pace, both in Bolivar County, and Belzoni, Humphreys County.

Deirochelys reticularia (Latreille).—Two specimens from two and one-half miles north of Hurley and two from six miles north of Vancleave, Jackson County, were taken. Bleached shells of two more specimens were found in a flooded field at the former locality. The largest specimen taken has a carapace length of 208 mm; the smallest, 114 mm. Two specimens have the characteristic dark vertical bars on the posterior surface of the femora, the rear surface of the thighs in the other two is immaculate yellow.

Lepidochelys kempii (Garman).—One specimen with a carapace length of 609 mm was secured off Chandeleur Island, Mississippi Sound, by the U. S. Seafood Commission and presented to us by Mr. Stewart Springer. A skull found on the beach at Deer Island and a juvenile, presumably from the Biloxi region, preserved at the laboratory in Ocean Springs are referable to this species.

The first mentioned specimen possesses five costal plates, the anterior of which is less than half the size of the succeeding plates; one claw on the front and two on the hind flippers; four inframarginals, the posteriormost of which is only half the width of the others; and 13 head plates surrounding the large median plate. The juvenile has a decidedly concave plastron. The specimen prepared by us was dark gray above and almost white below. The stomach of this large female contained appendages and shell fragments of crabs, *Callinectes* and *Hepatus*, and numerous shell fragments of gastropods.

Amyda ferox subspecies.—One specimen from Lake Washington, Washington County, is present in the Delta State collection but is not available at present for subspecific determination.

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Studies on the Natural History of the Unionidae

Max R. Matteson
University of Illinois, Urbana

Although many environmental features have become altered during the course of the past century, the family Unionidae has been able to maintain itself in a very satisfactory manner. The ability of this group to survive is emphasized by the realization that it suffers from a double handicap: its members are almost sessile and, furthermore, they are inhabitants of the substratum. The lowermost layer of water, the only stratum which mussels can utilize, usually lacks more features which are necessary for the maintenance of living forms than any other portion of an aquatic habitat.

Information on the life history of any animal is obtained by an assortment of methods. Some parts of it lend themselves to a statistical analysis so that results may be obtained. Other aspects can best be shown by charts or graphs. A large portion of a life history, which includes the study of ecological relationships, is gotten through a series of accurate observations. In this paper, simple mathematical computations have been necessary for various shell measurements, and in a few other instances. It is realized that the value of the results which are derived from direct observation depends upon the observer's ability to see and interpret natural phenomena accurately.

The writer gratefully acknowledges the aid given him by his sons, Max and John Matteson, in connection with the field work required for this paper. Their aptness in water combined with their acute vision were almost indispensable.

General discussion.—As one examines any stretch of water, either lentic or lotic, he soon becomes aware that situations exist in which fresh-water mussels are plentiful while in others they are lacking. After carefully studying the living clam in its natural habitat, he finds that one can predict the presence or absence of these animals at a location according to the environmental conditions existing at that site. They respond so fastidiously to several of the more important features which compose their environment that deviation one way or another from the optimum by one or more of these items will determine the presence or absence of the population at a given position.

Although there is some variation in the responsiveness of different species of clams to the individual environmental constituents, there is a striking uniformity of response by all clams in general to their surroundings. There are instances where general pollution of water has obliterated an entire population of clams from an area. For several successive years the author has studied the mussels in a small river near Urbana, Illinois. During the summer of 1951, a canning factory dumped refuse from its corn pack into a tributary of this stream. One month later an inventory of the same area studied before the contamination occurred showed only empty valves lying on the bottom. No living clams were found. Although some fish had been killed, many were still alive. The toxicity of the polluting materials had been potent enough to kill the mussels without having a lethal effect on most of the higher organisms.

As a family, the unionids have been able to perpetuate themselves in a

very satisfactory manner. This is especially true where natural conditions have always existed. Their ecological niche is relatively secure chiefly for the reason that no other significant fresh-water inhabitants eat plankton and suspended organic matter in appreciable amounts and, therefore, competition from that source is eliminated.

Because of their highly sedentary nature, they can be observed easily. An undisturbed population occupying a certain location, whether the site be the substratum of a lake or a body of running water, has been able to exist at that point because conditions have been favorable for its continuation. As long as these conditions remain static, the colony will exist indefinitely. Although limited movement by individuals may be observed, the colony will not change position. Variation among the almost infinite number of environmental factors determines the species present and their frequency. It has been observed by the author that there is little evidence of a space requirement for clams of any species. In some situations they occupy positions far apart while in others the individuals are often in contact with each other. This phenomenon would tend to prove that competition between species or individuals is negligible. It is believed that their food supply which is almost entirely planktonic is the predominating factor which determines their concentration at a given location. The physical and chemical aspects of the environment (e.g. temperature, dissolved oxygen, etc.) act individually as limiting agents on the concentration of a colony. Also, each factor must be present within its range of toleration for each species of mussel in the colony. If these factors can be tolerated, a higher intensity of plankton will then allow a greater concentration of mussels in a selected population. One or more adverse physical or chemical factors may exterminate the entire population thus involved because fresh-water mussels are unable to travel efficiently in a directional manner.

Modification of the environment of fresh-water mussels by human activities often upsets their life-pattern to the extent whereby they suffer severely. Coker *et al.* (1921) have shown that wing dams constructed in the Mississippi River have caused conditions to develop which are deleterious to the existence of clams throughout long stretches of water where they formerly existed in large numbers. The flooding of large areas of original river channel in the Tennessee River system by the erection of dams considered necessary for flood control has eliminated certain medium and large river species either completely or almost so from that system.

Pollution of various types has eliminated populations in many areas. It has been observed that elimination of the polluting factors in several of these sites has allowed the gradual return of mussels. Clam populations are so easily destroyed by most forms of pollution that the observation has been made that their dying in large numbers may be used as a crude indicator of pollution.

Cultivation of land adjacent to the many small rivers of central Illinois has almost eliminated clams in many areas. The resultant excessive silting both from fields and denuded river banks and the increased water temperature caused by the loss of shade which has resulted from the destruction of forest formerly occupying the river bank have probably been the most significant factors.

In the preceding paragraphs clam populations are said to be destroyed indirectly by the working of man. There remains one last factor which has been probably the most destructive of all: direct destruction of large numbers for commercial purposes. For many years the Mississippi River Valley was the chief site of the pearl button industry. During this time many button factories were located on the middle portion of the river, and its chief tributaries. The live mussels were dredged indiscriminately, only those whose valves made satisfactory buttons were utilized. The rest were thrown away. Eventually, depredations by clam fishermen caused the enactment of laws for the protection of clams during certain seasons of the year in many states.

Preadult ecology.—A study of the life history of a clam reveals that its presence or absence in any ecological situation depends on whether the positive aspects of its life cycle can predominate over those which are negative in nature. In the first place, many reproductive cells are formed by the female clam. The positive effect of this trait is counterbalanced by the fact that the spermatozoa of the male must travel varying distances through the water in order to reach the ova in the suprabranchial chambers of the female. Examination of the contents of the marsupial gill immediately following fertilization shows very few unfertilized ova (fig. 1). This condition is possible because tremendous numbers of sperm are formed throughout the year and then are held by the male until the females are ready to breed (Matteson 1948). The embryonic development, from zygote to glochodium, is carried on in the marsupium which, in turn, is housed inside of a formidable shell. This fact allows the safe development of upwards to 700,000 glochidia each year.

During this period the marsupium loses a portion of its efficiency as a respiratory apparatus. To prove this, 100 adult specimens of gravid and nongravid members of a dioecious species (*Lampsilis ventricosa*) were placed in
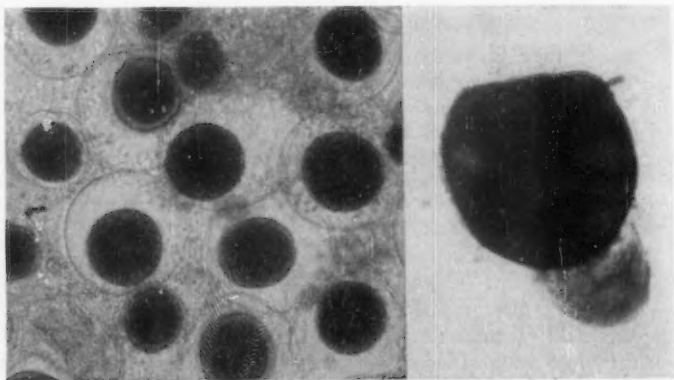
Figs. 1, 2.—1. (Left) Contents of marsupial gill of *Anodontoides ferussacianus* after fertilization. As each cell is surrounded by a fertilization membrane, fertilization has occurred and the cells are zygotes (130×). 2. (Right) Young of *Elliptio complanatus* within 5 minutes after dropping from the yellow perch (*Perca flavescens*). The foot is in a contracted position. It is able to extend twice the length of the shell and the tip is both ciliated and notched. The lighter spots represent the anterior and posterior adductor muscles. The piece of detritus designates the area of the inhalent siphon. There is no postglochidial shell growth in evidence (280×).

a covered container which was large enough so that all of the clams could be observed simultaneously. A post-mortem examination performed later disclosed a total of 33 gravid mussels, and 67 nongravid individuals of both sexes. The water temperature was then maintained at a temperature of 21°C for the duration of the experiment. When a specimen exhibited gaping valves which did not close upon prodding of the soft parts, it was considered dead and was removed. The dissolved oxygen content of the water was ascertained by the Micro-Winkler method at the time of death of each individual. The procedure was continued until 30 specimens, 18 gravid and 12 nongravid, had died. Evidence of rupture of gill tissue in three of the nongravid dead signified that they had shed very recently. A mean lethal threshold established for the gravid clams was approximately 1.8 cc of oxygen per liter of water higher than that of the nongravid ones.

Although no accurate statistics have been obtained on the lethal effects of increased water temperature on gravid clams, the author has noticed that when large numbers of live clams are kept in tubs, the first to die if the water becomes tepid, are usually the gravid females. This observation was made during a study of, *Elliptio complanatus*. As the tubs were well aerated at that time, oxygen concentration was probably maintained at a satisfactory level. Thus, we see that loss of gill efficiency, a negative factor, might cause the death of a gravid female, with the resultant loss of all the young.

As mentioned before, tremendous numbers of glochidia are placed into the water by the female. Ortmann (1911) states that some species eject glochidia in compact masses known as ovisacs which still retain the shape of the water tubes in which they were developed. The author has observed that several species mentioned by Ortmann have shed them singly or in small clusters normally, although ovisacs may be shed when environmental conditions have made the mussels uncomfortable. On several occasions, females of both *Lampsilis ventricosa* and *L. siliquoidea* have been observed shedding entire ovisacs. They were noticed in the spring and always in shallow water which had been overheated by unseasonable conditions brought about by intense sunlight. The intact ovisacs were scattered on the bottom near the adults. On another occasion, the mantle cavity of an aborting female, *L. siliquoidea*, was found to contain a leech slightly over one-half inch in length. Observation has shown that it is the usual practice for mussels to shed glochidia singly and moreover, over a period of one to three days, or even longer.

Those species which maintain a longer shedding period possess a definite advantage over the few who may shed ovisacs for a short time. Extensive experimentation by many workers has shown that mussels exhibit a marked degree of host specificity, usually using either one fish or, at the most, a few related species. When shedding occurs over an extended period, there is a greater chance that a suitable fish host may approach and become infected.

The glochidia of different species of clams possess various devices for maintaining themselves in a suspended condition in the water. Some possess a mucoid thread, the byssus. This may adhere to the fish long enough for the glochidium to attach itself to a fin. Repeated observations on live glochidia at hand show that they descend through the water in an opened condition, thus slowing downward movement. One interesting device employed by the

young of *Elliptio complanatus* was observed (Matteson 1948). In this in-
stance, mucoid material flowed from the exhalent siphon of the female in the
form of long, adhesive filaments which became attached to twigs projecting from
the bottom of the aquarium. Eventually, a cobweb-like structure was formed.
Individual glochidia, streaming from the exhalent siphon, adhered to the
threads. However, pitted against these and other unmentioned devices, is
the ominous fact that no suitable fish may pass by at an opportune time and
thus the whole group will perish.

Increase in either size or weight is negligible during the period of encyst-
ment. Examination of several hundred newly dropped immature clams has
revealed that externally no shell material has been added to the glochidial
valves during that time (fig. 2). However, the addition of materials to
the periphery of the original valves is rapid during the first several hours fol-
lowing excystment. Also, inspection of the soft parts through the nearly
transparent valves revealed that the original tissue had transformed itself
into the rudiments of the adult organs (fig. 3). Tucker (1927) shows the
young of *Anodonta imbecillis* as having developed post-glochidial shell, but
perhaps those specimens were gathered after existing in the free state for
several hours.

It is interesting to note that glochidia leave the female clam at a stage of
development in which they are unable to strive for themselves. With few
exceptions, the fins or gills of fish serve as "secondary marsupia." The tissue
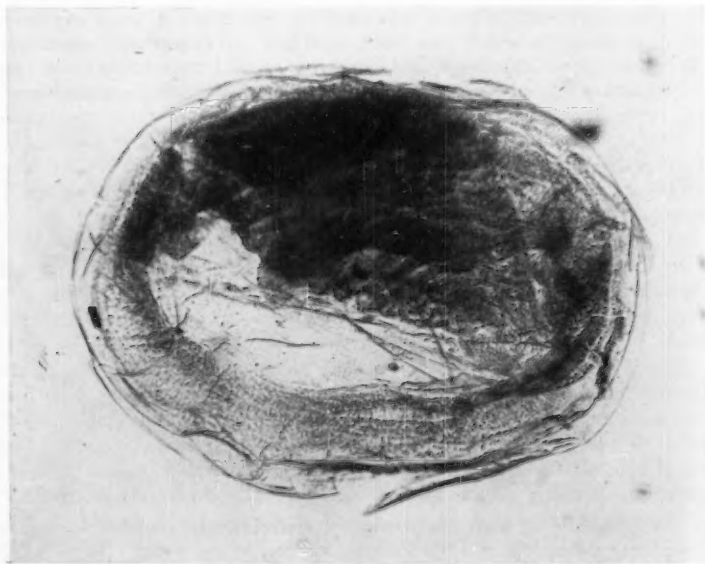

Fig. 3.—A 2-day immature mussel, *Elliptio complanatus*. The plumose gill-fundaments
are shown with development beginning antero-dorsally and proceeding postero-ventrally. At
this state the plumose appearance is caused by the incomplete fusion of the water tubes.
The inhalent siphon, visceral portion of the foot, and mantle are also in evidence (550×).

of the fish acts as a haven of refuge in which the glochodium undergoes the difficult task of metamorphosis completely isolated from possible enemies. Neither the true parent nor foster parent is seriously harmed by the embryonic mussels' presence in its body, unless unusual conditions exist (Murphy 1942).

Young mussels, still in their first summer's growth, are hard to find in nature. Further, it is next to impossible to locate them during the first few days after they have dropped from a fish. Therefore, the story of their existence in nature during the period soon after their leaving a fish is unknown and any discussion of their status at this time is a matter of speculation. Extensive screening of bottom materials in a small stream where large numbers of adult *Alasmidonta calceolus* were present failed to show young smaller than three millimeters. This length was attained during a period of two or three weeks after dropping, as ascertained by comparing their shells with older mussels in which the first season's growth could be easily identified. They were occupying the same area of substratum as the adults.

The possibilities of survival for newly dropped mussels in a lentic environment are greatly diminished when they are compared with those relating to shallow, running-water forms. This observation was made by the author after an attempt had been made to find young lake-dwelling mussels by examining bottom deposits. Very careful and highly concentrated searching with both Ekman and Petersen dredges on feeding grounds where known host fish were spending a major portion of their time failed to produce a single clam in its first summer's growth. The area where samples were taken varied from six to nine feet in depth. No older mussels were taken, although a large concentration of individuals representing four genera lived on and above the steep incline immediately above the area of lake-bottom which was sampled. An analysis of the dredged material showed bottom-ooze, mud, a mixture of decomposing aquatic plants and forest rubbish, and other detritus. A few of the young mussels which had been deposited in June were found later in the summer living with the adults. This study was made at Ocqueoc Lake, Presque Isle County, Michigan.

Fish are very liable to travel over large areas of substratum which is not suitable for supporting a clam population. The immature mussels are unable to prearrange a suitable "bailing out" period. As has been mentioned before, they may land on a bottom which is composed of any number of ingredients. Death may result from excessive silting or from several other agencies.

Certain protective devices are used to advantage at this stage of development by the young. It was noticed in the laboratory that they could reach the surface of the substratum when covered by fine silt as deep as three to four times their length. This was accomplished by movements of the foot which at this stage is from two to three times the height of the shell when it is extended (fig. 2). Also, the tip of the foot is ciliated and remains so for several days after dropping has occurred. It is notched at the tip.

Directional movement is effected by the newly dropped clam in a very interesting manner. With the cilia at rest, the foot extends full length. Then, with cilia beating rapidly, the notched tip seems to adhere to the nearest object at hand. The foot muscles then contract, thus moving the rest of the clam toward the fastened tip. The cilia then cease to beat and the tip of the

foot releases its grip, extends forward, and the process is then repeated. The young at this stage can climb smooth objects that are inclined sharply. This ability may help explain how the young are able to overcome certain barriers as they proceed shoreward. Nevertheless, only a small portion of the young starting the trip shoreward probably reach their destination.

After the young reach the shallow waters next to shore, their life-habits become the same as those of the adults who are already occupying the area.

Responses to aestivation.—Little concrete evidence has been obtained on the ability of fresh-water mussels to withstand the rigors of aestivation. Coker *et al.* (1921) mention that many mussels are killed by the partial or complete drying up of bodies of water. Isely (1914) found several specimens of *Uniomerus tetralasmus* which he had planted in a pond still alive when they were plowed up three months later after the pond had become dry.

On June 22, 1950, ten live, adult clams (*Lampsilis siliquodea*) were brought to the laboratory and placed on a table-top. The table occupied a position which allowed the clams to remain at room temperature during the summer. They were examined daily. The valves were tightly closed whenever they were observed. None attempted to alter position by extending the foot. The clams were kept under observation from June 22 to August 5. On the latter date all were opened by cutting both adductor muscles. All ten were alive. This fact was determined, first, by odor and, secondly, by the observation that there was contraction of the mantle as it was being cut from the valves. Effects of aestivation were best indicated by the condition of both the visceral and muscular portions of the foot. The latter was highly contracted and reduced in size. The visceral portion was also reduced in size, and later microscopic examination of its mass in crosssection showed a breakdown in tissue when compared with the body of a normal clam (figs. 4a, 4b). The tissues were fixed in Bouin's solution and stained with Heidenhain's hematoxylin with an iron-alum mordant. The lining of the mantle cavity at the end of the experiment had remained moist but the fluid present was very viscous. No attempt was made to differentiate between the effects of starvation and water loss. These two items operate inseparably in the case of fresh-water mussels as no feeding can occur during aestivation.

One disturbing factor in connection with the observations mentioned in the last paragraph is that the author has gotten identical results by examining members of a colony of 200 individually marked mussels which were placed in a strongly acidic lake with an hydrogen ion concentration reading ranging from 4.4-6.1 (unpublished data). The mussels were placed in the lake on June 23, 1943. Weekly observations were made during the summer. None of the mussels attempted to readjust their positions during this period. Those which were originally placed on the bottom ventral side up remained in that position. The valves were tightly closed whenever examined. No doubt, by doing this the individual mussels were able to maintain an alkaline state in the water contained in the mantle cavity for a longer period. In this case, the reaction of the mussels toward acidic water was similar to those toward aestivation. Loss in volume of body-parts would tend to imply that starvation was taking place, but the slow drop in pH within the mantle cavity may have been at least partially the lethal factor. At no time were siphons observed to be functioning.

Certain conditions were found to stimulate a clam undergoing aestivation to extend its foot. When several specimens were placed in a cool, moist environment, with no water present, extension of the feet began in a short time. Also, when other clams were placed in a sink where water was allowed to drip on their exterior, the muscular portion of the foot was often extended completely in an effort to establish a position by which movement could be

Figs. 4a, b.—(Top) Cross-section of a normal mussel (*Lasmigona costata*) showing healthy, ciliated, columnar epithelium of the digestive tract. The sinuses in the adjoining tissue are few and small in number (260×). b. (Bottom) Cross-section of a starved mussel (*Lasmigona costata*) which shows disintegration of the digestive epithelium. Also, cells have been destroyed in the adjoining tissue, causing larger sinuses (260×).

made toward the source of water. The slow movements of one clam usually did not cause withdrawal of the feet of the others in contact with it. At first, it was thought that the motivating element for the hydrotropic activity was the cooling effect of the water. This was disproved easily. Some clams were placed in a refrigerator. The temperature was then lowered gradually to 10°. Others, at room temperature, were placed in individual wire cradles in a position so that tap water could run over only the discs of the valves. In both cases the valves remained closed. Therefore, one may assume that the exposed borders of the mantle are highly sensitive to moisture. As soon as this organ detects the presence of either very moist air or water it initiates the procedure by which the foot is extended from the valves.

In nature, due to the sensitivity of the mantle's border to water, clams are seldom left stranded when the level of the containing body of water is lowered. On many occasions the author has observed clams moving down a gently inclined slope toward water, although the surface material had already become dry. Also, if they then came to a place where the slope proceeded upward, they invariably attempted to burrow deeply into the drying substratum in an attempt to remain in contact with water instead of climbing the inclined surface. They have been observed buried at depths of six inches in soft, coarse sand. If contact with water is lost, the mussel then closes its valves together tightly and begins the task of withstanding the period of dryness, assuming movement once again when the water level rises. This is the usual behavior of mussels throughout the middle and lower regions of the Mississippi River drainage system where there is excessive variation in water level.

Extensive observation has shown that the few, thin-shelled, toothless varieties of mussels cannot withstand drying out as well as those with thicker shells. On several occasions, in Michigan and Illinois, the author has observed drying stretches of exposed bottom where mussels had been out of water for long periods of time. Most of the heavy-shelled genera (*Lampsilis, Amblema, Cyclonaias,* and others) were well buried and alive. However, the genus *Anodonta* was seldom completely embedded in the substratum and many specimens were dead and decomposing. This disability, and its inability to withstand a comparatively rapid current, especially at times of flood, are perhaps the only reasons why this genus is usually limited in numbers in the rivers of Illinois while it is listed as one of the most common clams in the lakes of Michigan.

Responses to temperature.—Significant stages in the reproductive cycles of fresh-water mussels are directly dependent on the temperature of the surrounding waters (Matteson 1948). When the rise in water temperature is retarded in the spring, both the development and deliverance of spermatozoa into the water through which they travel is retarded proportionately. In like manner, oögenesis is slowed.

Examination under the microscope of the soft parts of *Elliptio complanatus* cut in cross-section, representing samples of clams taken from nature weekly for a period of two years, showed that the dates of the various stages of sexual activity varied each year; but this variation was always in direct relation to the water temperature. One season, the summer of 1945, exhibited so small a rise in temperature that only one female clam was found with viable glochidia throughout the entire spring and summer. Large numbers of clams were

opened during that summer but all, other than the one, showed embryonic development which varied from early cleavage to a stage where the glochidial shell had begun to form. The egg membrane was always observed to be intact. Normally, this membrane (egg shell) must be ruptured and lost before the glochidium leaves the parent, otherwise attachment to a fish is impossible.

Indirectly, temperature conditions wield a strong influence on the life of a mussel by determining both the intensity and length of availability of its food supply. All fresh-water mussels feed entirely upon plankton. The concentration of a plankton population is dependent upon the temperature of the water in which it exists. Phytoplankton, especially, is concentrated in direct proportion to the intensity and duration of sunlight. The latter item, in turn, allows the water temperature to rise and fall in a corresponding manner. During the colder months of the year, a mussel is dormant and consumes little if any food. As a result, shell formation is almost nonexistent during this period and the narrow layer which is formed is indicated exteriorly by a darker band of periostracum. Microscopical examination of the lumen of the alimentary tract for this period shows little material present which can be used for food. The period including early and middle summer normally allows the greatest growth of shell and corresponds with the period when plankton populations are at their peaks. This phenomenon is easily observed in young clams and, more easily, in those experiencing their first summer's growth. As fall, with its lowering temperature, approaches, growth is retarded.

An analysis of literature shows that there is considerable divergence of opinion as to the behavior of fresh-water mussels during winter. Van der Schalie (1938) states that they do not migrate into deeper water but merely embed more deeply in the substratum. He was able to follow movements of the mussels by attaching a metal disc for identification by wire through a hole bored in the valve of each mussel. Evermann and Clark (1917) tend to show the opposite viewpoint, that mussels migrate into deeper water during the winter months. Van der Schalie's experimentation was done on a river while their investigation was performed on an Indiana lake.

As indecision had existed on winter movements among mussels, it was decided that a further attempt at research on the subject should be made so that data might be gathered which would support one or the other viewpoints. A lake was selected in northern Michigan which possessed the required features of being far enough north so that cold winter conditions would prevail for an ample period of time and large and deep to the extent that no disturbing influences would alter the effects of temperature (Bar Lake, Manistee Co., T24N, R16W, S10, 15, 16). A stretch of shoreline was then selected where there was a sandy, gently sloping shelf extending outward approximately 24 feet to a depth of four feet and then terminating sharply with a drop of about ten feet to the deeper lake basin. A site near the outlet into Lake Michigan, 300 yards away, was selected with the thought that a very slow, constant flow of water would be preferable to still water.

On November 21, the water temperature was 10°C. Twenty adult specimens of *Lampsilis siliquoidea* were selected nearby at random. The substratum was examined around each clam which was to be used in order that any recent movement toward deeper water might be recorded. No tracks were in evidence. By means of a three-cornered file, grooves were cut in the

valves to form individual symbols for identifying each clam.   This method of
identification had worked excellently in earlier experimentation where individu-
als were to be studied (Matteson 1948).   Starting at a depth of one foot,
four lines of five stakes each were placed in water in a position roughly parallel
to the shore at one-foot intervals in depth, with the outer row falling near
the edge of the declivity (fig. 5).   They were lettered to correspond with the
symbols representing letters found on each mussel (fig. 6).

The system of symbols and the method for placing them on the shell has
been employed by the author for many years and has been highly satisfactory
at all times.   As other workers may wish to use it, an explanation may be
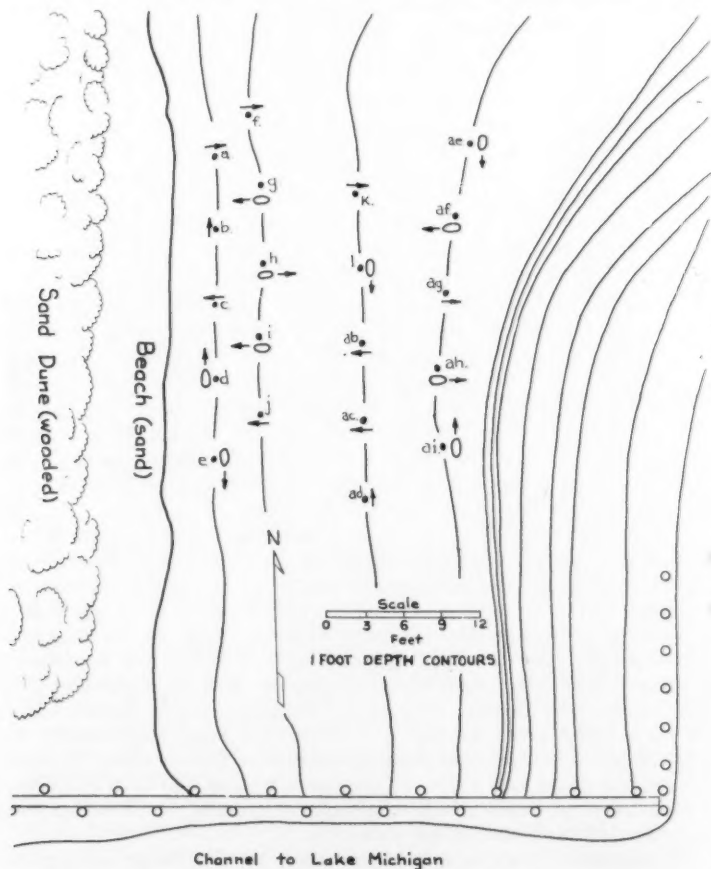
Fig. 5.—Map of staking experiment. The solid black circles represent stakes. An
arrow only by a stake means that the mussel was placed in a normal position with anterior
end pointing the direction of the arrow. An oval signifies that the mussel was placed,
unburied, on its side, with the anterior end pointing in the direction shown by the arrow.

justifiable at this time. Single file-marks on one designated area only of either valve symbolizes a given letter. Thus, clams may be lettered from *a* to *l*. If more symbols (clams) are needed, a combination of two single file-marks on two areas may be used, as *ac*. Then, if still more mussels are needed, double file-marks on one area may be used; thus, we have *aa*; then, with double combinations, *aagg*; and so on, until an almost limitless number of symbols are possible.

The mussels were placed against the stakes in various positions (fig. 5) and the site was abandoned for the winter season. Ice covered the lake completely on December 18. The ice cover was reduced to masses of ice-fragments by March 28. The winter was judged to be a normal one for that region.

On April 10, the site was revisited. The water temperature above the clams was 8°C on that date. Following this paragraph is an account of the mussels' positions at the time of recovery.

Specimens *a, b,* c, *e*. Both stakes and clams had disappeared. Evidently, ice had frozen deeply enough so that the row of clams stationed at the one-foot depth had been enveloped by it. The ice mass must have broken from the shore as a solid sheet because the stakes had also disappeared. The clams were never found.

Specimen *d*. Stake gone, specimen found on its side, paritally embedded, foot extended, no track in evidence; 1 foot N.E. of stake *ac*. It probably had dropped from the ice at this point.

Specimen *f*. Embedded, no track, foot extended.

Specimen *g*. Position unchanged from fall (clam alive).

Specimen *h*. Track evident, specimen 9 inches lakeward from stake; embedded, normal postion, foot extended.

Specimen *i*. Track evident, clam had moved in semicircle to position 3 feet north of stake, normal position, foot extended.

Specimen *j*. Position unchanged, foot extended.

Fig. 6.—Two left valves of *Lampsilis siliquoidea* showing areas of letter-symbols. Where few specimens are needed, single file-marks at the designated location are sufficient. Where many specimens are needed, double marks may be used. The right valves, not shown, are lettered to 1.

Specimen *k*.   Track present, moved N.E. 1½ feet, embedded, foot extended.

Specimen *l*.   Almost on side, partially embedded, moved length of shell, foot extended.

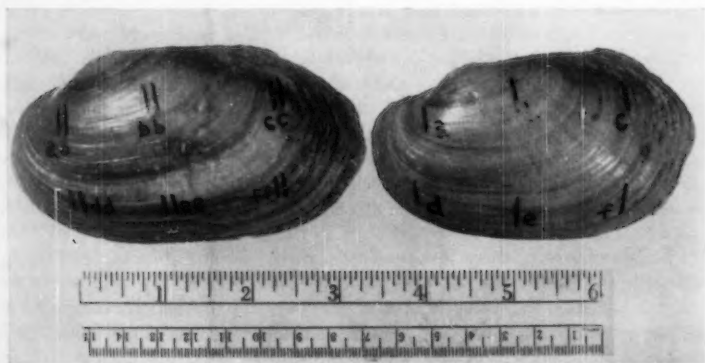Specimen *ab*.   Although originally placed in a normal, embedded position, the clam had moved about 6 inches shoreward, and had turned almost on its left side, foot extended.

Specimen *ac*.   Position unchanged; foot not extended but clam was alive.

Specimen *ad*.   Position unchanged, foot extended.

Specimen *ae*.   Embedding taking place, foot extended, but no directional movement.

Specimen *af*.   Track shoreward 2 feet in light curve toward north; clam in normal position, foot extended.

Specimen *ag*.   Position unchanged, foot extended.

Specimen *ah*.   Clam moved lakeward length of shell during embedding process.

Specimen *ai*.   Movement ½ foot north from stake, normal position, foot extended.

There was no accurate way for determining whether the tracks were made in the fall or spring, or at both periods, other than the presence or absence of sediment in the groove and the acuteness of the angle at its apex.   However, observations made following the planting of 2000 marked clams which are being used in other experiments show that there is a short period of restlessness present immediately after they are placed in a new location.   No doubt, their being handled stimulates them into a more or less mechanical reaction which involves movement.   This fact would tend to show that the tracks were made in the fall.   At any rate, this experiment shows no evidence of migration into deeper water by *Lampsilis siliquoidea* during the winter.

The point might be suggested that migration may take place at an earlier period in the fall than the time when the just-described experiment was initiated. Several other observed phenomena definitely refute this conjecture.   At the time in question, the substratum would necessarily be furrowed with many tracks, all tending eventually to end over the edge of the declivity.   This phenomenon would be again present in the spring.   Repeated observations made during both seasons for several years have failed to disclose any evidence supporting seasonal migration.   In fact, tracks are not commonly found on a substratum at any season where the clams have not been disturbed by man or unusual natural conditions.

In a river system, there is a tendency toward increased movement among mussels as the headwaters are approached.   This is especially true where the current is definite, the water clear and shallow, and the bottom composed of sand or a mixture of sand and gravel. . In this situation there would be a paucity of planktonic food, the water temperature would be highly variable, and the clam is able to move easily through the bottom materials.   As conditions are usually more static in the lower reaches of a river there is less reason for movement.

During those years when a stock pile of clams was required for winter

study of various naiad features, large numbers of *Elliptio complanatus* were concentrated several-deep around a stake which was driven firmly into the bottom in about three and one-half feet of water. The reservoir of mussels was established at Douglas Lake in northern Michigan during September. As one dozen specimens were removed each week, even after the ice-cover had formed, any movements could be observed quite easily. As no clams of this species occurred naturally in this lake, there was no chance of mixing them with wild representatives. During April, after the ice-cover had disappeared, it was definitely observed that little movement had taken place and none were recorded to have descended down the 60-foot declivity which began no more than ten feet lakeward from the pile. It is well to note, however, that all references included here are concerned with lentic waters.

Responses to currents and flooding.—Van der Schalie (1938) upon studying the distribution of fresh-water mussels in the Huron River in southeastern Michigan, found that each mussel had selected as its habitat a more or less specific region of that river. An analysis of the habitats of all clams occupying the Huron River led him to believe that any river of considerable size which contained mussels could be divided into several regions, according to their patterns of distribution. He noticed that some mussels were found throughout the length of the river while others occupied only certain well-defined stretches of water. Other than under certain anomalous conditions, Van der Schalie's observations are extremely accurate.

During the years 1947-51, a survey was conducted on the headwaters of the Mackinaw River (Ford and McLean counties, Illinois) to determine the clam populations of that area. This river originates as two small drainage ditches. Both flow into a larger, common one. All were dug about 30 years ago. They usually follow the stream-beds of creeks from which the river formerly had its beginning. In order that drainage could occur rapidly, the ditches follow a straight line as much as is possible. The two branches of the stream begin abruptly and maintain a width of five to eight feet and a depth of six inches to two feet for about one-half mile to the point of confluence. From this point, there is a stretch of approximately one mile of almost straight ditch where the width is from eight to ten feet and the depth is from two to four feet. From this point onward, the river is no longer dredged and further, it assumes the characteristics of a small river, according to Van der Schalie's definition. For convenience's sake, the two tributaries shall be defined herein as representing a small creek environment and the larger, single stream, a large creek environment. The substratum of both creek-types is composed of sand, with a mixture of sand and gravel where the water runs more rapidly. Surprisingly, there is little silt in evidence, either in the tributaries or along the one mile of dredged stream.

Enough time has elapsed since the construction of the ditches so that at present day normal stream conditions once more exist. Along the length of the ditches, various small tree-trunks and brush have fallen into the water so that there are a number of holes, often as deep as four feet, and sand bars throughout its length. During flood stage, the surface of the water has been measured as being 17 feet higher than normal. This is due to the levelness of the surrounding land and, therefore, the resultant difficulty with which the water is able to seek a lower level. Thus, any clams occupying the bottom

are subjected to both the effects of scouring and silting. Evidence of the intense action of the former factor was noticed when a winter's supply of *Alasmidonta calceolus* which was being used by one of the author's doctoral students for winter research was swept down the creek, although it was contained in a well-built, anchored cage. The bottom after a period of flood is often quite different from its former condition. As a result of the just-described phenomenon, one may say that any population of mussels occupying this area must exhibit a high degree of perseverance.

The total populations and ratios between species were probably similar in both small-creek tributaries. A· representative inventory was obtained from one tributary. Beginning at the point of confluence, the writer walked in the water to the uppermost end of the ditch. When a mussel was detected, it was examined, recorded, and replaced. The inventory included the following species: *Actinonaias ellipsiformis* (83), *Alasmidonta calceolus* (23), *Anodontoides ferussacianus* (11), and *Strophitus rugosus* (1). All were decidedly smaller than specimens found down-stream.

A survey of the large-creek environment, from the point of confluence to the end of the drainage ditch (one mile), produced the following species: *Anodontoides ferussacianus* (84), *Alasmidonta calceolus* (48), *Actinonaias ellipsiformis* (22), *Strophitus rugosus* (18), *Lampsilis siliquoidea* (2), *Uniomerus tetralasmus* (2), and *Anodonta grandis* (1). *U. tetralasmus* has been considered as occurring least frequently of any mussels in this habitat.

It is surprising to note that the most common inhabitant of this environment is *A. ferussacianus*, which possesses one of the thinnest shells of any mussel. This clam was always observed embedded in the substratum to the extent that only the umbones of the highly obese dorsal portions of the two valves were exposed to the water current, thus maintaining a position which was flush with the surface of the substratum. It is because of this condition that the clam is able to withstand the powerful currents sweeping over it.

Other small and large-creek mussels have also developed body structures so that they may withstand strong currents. Outstanding among the modifications is the presence of a truncate condition. In the headwaters, *Alasmidonta calceolus* embeds deeply enough so that the highly truncate posterior end is flush with and lies in the same plane as the substratum. At other points along a river, wherever strong currents exist, we may find the genera *Truncilla, Plagiola, Dysnomia,* and *Alasmidonta* (other species than *calceolus*). All of these naiades are highly truncate. Then, there is the mussel, *Elliptio spinosus,* found in a few of the short, rapid streams of southeastern United States, which has developed valves possessing several long spines. These structures tend to prevent the mussel's rolling along the bottom. Still other shell features have been developed so that better contact with the substratum may be maintained: some species are pustulose, others, costate, and still others, tuberculate.

An inspection of the preceding inventories shows that all clams present in those lists are relatively thin-shelled. At first hand, this trait may appear as detrimental in resisting current until one realizes that the resulting lightness of total body will not only facilitate the clam's burrowing out of the bottom after being covered during a period of flood but will also allow it to settle near the surface as sand, gravel, silt, and other heavier materials settle to the

bottom more rapidly during that period. The heavier-shelled naiades, unless they possess special structures for combating both currents and the dangers of a shifting substratum, cannot exist in headwaters. However, certain interesting situations are brought to mind which may seem to contradict this opinion. During an inspection of a tributary of the Sangamon River (Champaign County, Illinois), one such situation arose. The tributary is merely a short, narrow ditch five feet in width and two feet in depth which runs sluggishly through level fields to the main river two miles away. The water moves very slowly. In a distance of 100 feet, 46 dwarfed, adult specimens of *Amblema costata* were found in the silt-covered bottom. The extreme levelness of the surrounding land signifies that even during flooding there probably is little increase in current. Thus, this heavy-shelled mussel has less difficulty remaining above the silt during that period. *A. costata* is typically a small to large-river inhabitant. On another tributary of similar proportions, which entered the Sangamon River about one mile below the just-mentioned one, a small pool eight feet in diameter is formed above a road culvert only about 300 yards from the creek's source. In this situation, 21 extremely dwarfed specimens of *Lasmigona complanata* (fig. 7) were collected. The dwarfed condition is probably due to the low plankton content of the water. This mussel is typically a small to large-river inhabitant. Baker (1928) states "it seems equally abundant in both large and small rivers and creeks." He also states that the "large and small stream forms do not differ materially, though the Mississippi form is smaller than the creek forms." This opinion is not held by the author who feels that many field observations prove that the reverse is true, with the smaller specimens of *L. complanata* living in the small rivers. As with *Amblema costata*, this mussel is found living in the just-mentioned environment

Fig. 7.—Dwarfing caused by a limited food supply in *Lasmigona complanata*. The smaller valve possesses approximately the same number of growth lines as does the larger one.

because the water current is never strong enough to cover it deeply with bottom materials. One interesting deduction which one can draw is that the fish host of both these mussels must be able to exist in the headwaters of a river if special conditions prevail there as well as farther downstream, or else, another fish assumes the role of host in the former habitat.

A seemingly anomalous situation exists in the large-creek habitat of the Mackinaw River in that *Anodonta grandis* is present in restricted numbers. Baker (1928) mentions that the subspecies *plana* occupies creeks in Illinois. However, the specimens in question are much larger than those mentioned in his description. No explanation can be given for its presence. This species normally occupies slow-moving or standing water. None were deeply embedded.

Another mussel, very similar in general form to *A. ferussacianus* and *A. grandis* but with heavier shell, is also present in the large-creek environment, *Strophitus rugosus*. If any of these mussels were to be uncovered by unusually strong currents such as those present during a stage of flood, they would be carried down the stream for varying distances. Eventually, they would roll into an area where currents were eddying in such a manner that downward progress would be halted. This reasoning would seem to show that the area formerly occupied by them would become depleted of these species, but it must be remembered that, simultaneously, clams from higher up the creeks will take their place, infected fish will drop young individuals, and the population will remain constant.

It is next to impossible to enumerate accurately any one factor or even a specific list of several of them which will determine the presence or absence of a species of mussel in either standing or running water. One cannot overlook the fact that the distribution of a fresh-water mussel is dependent upon the distribution of its fish host. Even though conditions are ideal for a species of mussel to exist at a given site, it cannot live there if its fish host is unable to cope with that environment. Several riffles on the lower Mackinaw River were found to have approximately the same water velocity as the large-creek environment. Of the mussels mentioned in that inventory, *L. siliquoidea, A. ferussacianus,* and *S. rugosus* were found to be present; the others were not, because the fish hosts are probably lacking there. *A. grandis* was found in the quieter waters nearby. Because it offers more resistance to the current, *A. grandis* is unable to occupy the riffles at that site. Other than the mechanical effect of pressure, it is doubtful if water current alone has any other direct effect on fresh-water mussels. Indirectly, it is highly desirable, if moving at the right velocity, because it delivers life-giving materials to the almost sessile unionids, such as food, oxygen, and other substances. However, it may cause their extermination by depositing materials so that they are asphyxiated.

Another phenomenon which is certainly as striking, if not more so, as the distribution of mussels along a river's length is the variation in their size at different points along that river. It is a well known fact that the total plankton count is lowest at the headwaters of a stream, unless a standing body of water enters at this point. There is a gradual increase in plankton as the river becomes larger, with a maximum amount present at the mouth where the water has lowest velocity. Assuming that an available food supply is the chief factor in determining the size of mussels, those of most species will increase

in size as a river becomes larger. This observation is well substantiated by evidence gained from surveys made by the writer on several rivers in Illinois, especially the Mackinaw, Sangamon and Embarrass. Probably, *Anodonta grandis* fits least into this picture and naturally so, because most authorities describe it as normally occupying either standing or slow-running water which possesses a soft substratum.

There is a tendency on the part of many species of mussels which occupy river systems to be compressed in headwaters and to become more obese as they progress down the rivers. This observation was made by Ortmann. In his discussion of it (1920) he states that with a loss in obesity there is a gain in length and height. None of his examples are typical small stream forms. Although he lists a considerable number of species which illustrate the law, he states that many other varieties manifest little or no change in obesity. Ball (1922) substantiated Ortmann's observations partially by making a mathematical study in which he correlated stream flow and obesity using most of the mussels mentioned by Ortmann. However, he does not conclude that there is a tendency toward a change in height and length at different river levels. The exact cause of obesity is still unknown. It probably is not determined by rate of current alone but a combination of several factors. The writer feels that in a species which responds to the law, the genetic potentialities for obesity are always present and that the environmental factor of water velocity, perhaps combined with the amount of food present, determines the degree at which the trait is manifested.

Responses to silting.—It is a long accepted fact that excessive silting will either completely obliterate a mussel population or limit it to a very few species. Invariably, they are extremely light-shelled and obese. Several species of the genus *Anodonta* are able to float at the water's surface. Extreme lightness in body weight and the ability to hold the valves tightly closed for long periods of time seem to be the only adaptations present among mussels for combating silting.

One striking illustration of mussels living in a silt-like environment successfully is brought to mind. French Lake, in Emmet County, Michigan (T39N, R4W, S26, 27, 34, 35), is connected to Lake Michigan by a stream about one mile in length. The area of the lake is about one and one-half square miles and it is contained in a basin of sand and gravel. A vast accumulation of highly flocculent, minutely divided, humic material, often 15 feet in depth, is present in the northern half of the lake. On a quiet day, there is a layer of highly transparent water about one foot in depth over the apparently hard surface of this mass. The pH of the layer of water is approximately 8.0. With eyes shut, one can introduce an arm or leg into the bottom full-length with no knowledge of doing so other than detecting a sharp decrease in temperature.

When one stands in a boat and scans the surface of the silt bottom he sees an astonishing sight. Within the limit of vision, the bottom is pitted with innumerable cone-shaped depressions, often with three or four present in an area of one square yard. Each depression is from two to three inches in both diameter and depth. The apex of each cone is formed by the two siphons of a mussel, *Anodonta cataracta*. The shell of this mussel is so thin that a live specimen can be easily crushed in one's hand. Probably, during periods when

the water is turbulent, the mussels sink to a depth where their density equals that of the silt and then float or crawl up to the surface of the silt bottom after it has once again settled.

Summary.—Although there is a certain degree of variation in the response of individual species of mussels to their environment, all mussels react similarly to most factors.

Competition between individuals or species for food is very limited. However, their numbers have been diminished by man, indirectly, through the alteration of natural waters and, directly, by being the source of buttons and other commercial products.

As fresh-water mussels produce tremendous numbers of spermatozoa, ova, and glochidia, they are able to overcome the hazards associated with reproduction. These include loss of spermatozoa during their passage to the female through water; fatalities resulting from the possible absence of a proper host fish; and losses suffered during the trip to the site of the colony of adults.

During the period when part or all of the gills act as marsupia, the female mussel becomes more sensitive to a lowered oxygen content of water and increased water temperatures.

Fresh-water mussels, in general, release glochidia into water either singly or as small clusters. Intact ovisacs are released only under abnormal conditions.

The glochidium undergoes complete metamorphosis without evidence of growth while encysted in a fish gill or fin. A need for protection is the chief reason for encystment.

Most fresh-water mussels are well equipped for undergoing long periods of aestivation. This trait has allowed them to occupy successfully rivers which exhibit great fluctuations in water level. Without this asset, the Mississippi River drainage system would be quite devoid of them, instead of being the center of the world's unionid population.

When the mussel is out of water, the mantle border is responsible for detecting moisture. Atmospheric effects on only the valves do not promote movement of the foot.

Completion of the annual reproductive cycle among naiades is highly dependent upon a favorable annual temperature cycle.

Evidence at hand shows that *L. siliquoidea*, and probably other clams in general, do not migrate to deeper water nor embed significantly during winter in lentic waters.

Mussels with shells of medium weight are more successful than those possessing heavy shells for living in headwaters of streams because they are less liable to be buried during periods of flood. Some mussels withstand current by being truncate, costate, tuberculate, pustulose, or spined.

As many species of mussels progress toward the headwaters of a river, they become less obese and smaller in size.

In order to live in a very soft substratum, the density of a mussel's body must be equivalent to, or perhaps less than at times, that of the substratum.

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The Anatomy of the Feeding Apparatus of Uropoda agitans Banks, 1908, a Mesostigmatid Mite

Flora E. Gorirossi*

University of Maryland, College Park

In a recent paper Gorirossi and Wharton (1953) described the feeding apparatus of *Megisthanus floridanus*. This description was prepared for the express purpose of serving as a model for the description of other mesostigmatid mites. The terminology adopted in that paper was based not only on a knowledge of *M. floridanus* but also on a study of seven of the eleven phyletic lines recognized as comprising the Mesostigmata (Baker and Wharton, 1952). The present paper is the second of a series on the anatomy of the mesostigmatid gnathosoma and is concerned with *Uropoda agitans*. This species is a representative of the group Uropodina, a line that is quite distinct from the Megisthanina—the group to which *M. floridanus* belongs.

U. agitans was chosen as the second form to be described because it differs so markedly from *M. floridanus*. Despite the lack of superficial resemblance between the two forms it has been possible to use the same terminology in describing both of them. The methods discussed in the paper on *M. floridanus* were used in the present study.

Habits.—Specimens of *U. agitans* were originally reported from the nest of the Argentine ant, *Iridomyrmex humilis* Mayr, in Baton Rouge, Louisiana in 1908 by Wilmon Newell. They were sent to Banks who described and named them. Since then they have been recovered from dung and have recently been associated with damage to commercial earthworm beds. In the laboratory they are kept in small culture jars and fed once or twice a week on ground Purina dog checkers. They measure about 960 microns long, are ovoid to round in shape and dark brown in color. The immature stages are of the same general appearance as the adults but either have no color or are a pale yellowish-brown. When the mites are feeding they place a particle of food in front of them between their first pair of legs and use their other legs for support, or, if the piece of food is relatively large, they may use all four pairs of legs to hold it. The first pair of legs are kept in rapid movement, feeling the surface about them. If the mites are starved for a few days, as many as fifteen mites will gather about a particle of food in an attempt to feed. While feeding, the chelicerae begin a continuous process of protraction and retraction, each moving in alter-

nate directions. The conduction of the food towards the mouth has not been observed. It would seem, however, that the digits of the chelicerae would shear the food and that the umbrella-shaped excrescence on the digit of the second segment would then convey it to the mouth. When the gut contents from a mite which has just finished feeding are examined many minute particles of food can be seen.

Gnathosoma.—The gnathosoma of *U. agitans*, unlike the freely articulating gnathosoma of *M. floridanus*, is largely concealed from a ventral view by the broad, flat coxae of the first pair of legs which project in a vertical plane over the ventral surface of the gnathosoma. It is concealed also from a dorsal view because the dorsal wall of the idiosoma extends well beyond it. As a result of the encroachment of the coxae of the first pair of legs over the ventral surface of the gnathosoma, the gnathosoma is greatly compressed and much reduced. It and the coxae of the first pair of legs can be withdrawn into the idiosoma by strong muscles which insert on their bases (Pl. I J; II F, G). The skeletal elements connect with the rim of the camerostome at the anterior, ventral level of the idiosoma by means of two synarthrodial membranes. One of the synarthrodial membranes encircles the proximal edge of the gnathosomal ring. It connects the dorsal and lateral walls of the gnathosoma directly with the dorsolateral margins of the camerostome; ventrally, however, the membrane connects it to the proximal, dorsal edge of the coxae of the first pair of legs. Articulating with the gnathosomal synarthrodial membrane immediately dorsal to the gnathosoma and ventral to the extension of the dorsal wall is a broad, triangularly-shaped, tectum-like structure. The other synarthrodial membrane is attached to the proximal edges of the coxae and connects the coxae with the ventral rim of the camerostome. The coxal membrane meets the gnathosomal membrane laterally and jointly they fuse to the rim of the camerostome, so that the cavity of the camerostome is completely closed. Berlese described, in part, the relation between the gnathosoma and the camerostome in 1903.

The ventral surface of the gnathosoma along its mid-line measures approximately 184 microns. Of this, the gnathosomal base occupies less than half of the posterior portion (77 microns). Anteriorly is the hypostomal region (107 microns). The palpal trochanters of *U. agitans* are unusually broad and lie flatly at either side of the hypostome. Their extremely long setae resemble movable tentacles.

Gnathosomal base.—(Pl. I A, I, K) Except for the deutosternum and the gnathosomal setae, the gnathosomal base is void of ornamentation. Contiguous with the ventral walls of the gnathosomal base anteriorly are the broad walls of the hypostome; the trochanters of the pedipalps articulate with its lateral walls, and from its dorsal surface is joined the truncated tectum.

Deutosternum.—(Pl. I I, K) The deutosternum of the female differs markedly from that of the male, but in both sexes the ornamentation of the deutosternum is restricted to the anterior half of the gnathosomal base. In the female the ornamentation consists of three tranverse rows of fine teeth (15-20) which are directed anteriorly. The rows are evenly spaced from one another. The most anterior row of teeth differs slightly from the others. It is actually formed by two anteriorly projecting, arc-shaped lines of teeth which meet at the mid-line of the deutosternum to form a "v." The ornamentation
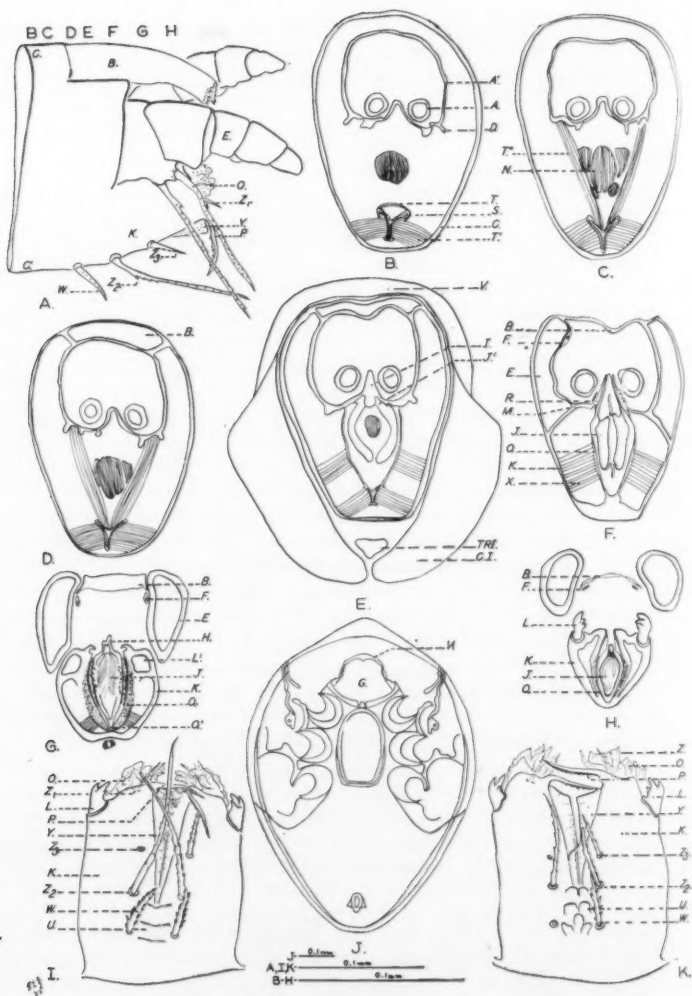
PLATE I

Lateral view of gnathosoma of a female *Uropoda agitans;* B-H. Cross sections of the gnathosoma at levels indicated in fig. A; Figures A-F are of a female sectioned at 10 microns; Figures G-H are of a male sectioned at 8 microns; Figure E shows relation between tritosternum, coxae I and dorsal, tectum-like structure; I. Ventral view of gnathosoma of a female; J. Ventral view of idiosoma of a female with first pair of legs, tritosternum and gnathosoma removed to show camerostome; Ventral view of gnathosoma of a male. LEGEND: A, chelicerae; A′, internal sheath of chelicerae; B, tectum; C-C′, gnathosomal base; C I, coxa; D, subcheliceral plate; E, palp; F, salivary stylus; G, camerostome;

of the deutosternum in the males consists of a series of paired and unpaired, anteriorly-projecting, crescent-shaped lobes. Unlike the lines of the first row of teeth in the deutosternum of the female, the lobes of the male never meet along the mid-line. Usually, there are three paired and a single unpaired lobe. The unpaired lobe, if present, occurs in the mid-line just anterior to the most posterior pair of deutosternal lobes and is always provided with teeth. The paired lobes may be with or without teeth. On most of the specimens examined the two anterior pairs of lobes lack teeth while the most posterior pair possess them.

Gnathosomal setae.—(Pl. I I K)   The gnathosomal setae of the male are more delicate than those of the female. They are slightly narrower and have fewer setules. In the male they are about 40 microns long and have about 10 setules. They are always found closely applied to the most posterior pair of deutosternal lobes. In the female they are about 40 microns long and have about 40 setules. They are always closely associated with the most posterior row of deutosternal teeth.

Horizontal shelf—(Pl. II A)   The horizontal shelf of *U. agitans* differs markedly from the shelf found in *M. floridanus*. In *M. floridanus* only about one fifth of the shelf extends into the idiosoma; in *U. agitans* only about one fifth of the shelf is restricted to the gnathosomal base. The remainder extends into the idiosoma as far as the metapodosomal portion. The components of the shelf (subcheliceral plate, epistome and tentorium) will be considered separately.

Subcheliceral plate.—(Pl. I B; Pl. II A)   The posterior four fifths of the subcheliceral plate projects into the idiosoma to about the metapodosomal portion. The bars of the plate do not lie parallel with the horizontal plane of the body of the mite but tilt laterally. Their medial portions are more heavily sclerotized than their lateral portions. They connect posteriorly by means of a lightly sclerotized bridge, the ventral surface of which serves for the origin of the epipharyngeal muscles.

Epistome.—(Pl. I E)   The degree of sclerotization of the epistome in *U. agitans* is much less than in *M. floridanus*. It does not support the labrum as the epistome does in *M. floridanus*, instead, its medial, ventral surface is contiguous with the dorsal wall of the epipharynx and the labrum is fused with the proximal edge of the dorsal wall of the epipharynx.

Tentorium.—(Pl. I F; II A)   In *U. agitans* the tentorium unites the sides of the epistome and the most distal lateral surfaces of the subcheliceral plate with the gnathosomal ring.

Internal and external cheliceral sheaths: The arrangement of the internal and external cheliceral sheaths of *U. agitans* is the same as described for *M.*

H, labrum; I, epistome; J, epipharynx; J', base of epipharynx; K, hypostome; L, corniculus; L', base of corniculus; M, tentorium; N, epipharyngeal muscles; O, hypopharyngeal processes; P, hypostomal processes; Q, wall of hypopharynx; Q', hypopharyngeal groove; R, hypopharyngeal stylus; S, pharynx; T, pharyngeal constrictor muscles; T', pharyngeal dilator muscles from gnathosomal ring; T", pharyngeal dilator muscles from epistome; Tri, tritosternum; U, deutosternum; V, tectum-like structure dorsal to gnathosoma; W, gnathosomal seta; X, hypopharyngeal dilator muscles; Y, protosternum; $Z_{1, 2, 3}$, distal, "medial," and "lateral" hypostomal setae.

floridanus. They differ from those of *M. floridans* only in their increased length which serves to accommodate the long chelicerae.

Pharynx.—(Pl. I B-D)   The pharynx of *U. agitans* in transverse sections shows a triradiate lumen.   Seven pairs of dilator muscles which originate from the walls of the gnathosomal base insert on its ventrolateral walls.   These alternate with constrictor muscles which run from one corner of the pharynx to the other.   Originating from the ventrolateral walls of the epistome are additional dilator muscles which insert on the dorsolateral walls of the pharnyx.

Mouth.—The description of the mouth given for *M. floridanus* can also be applied to the pharyngeal opening found in *U. agitans.*

Tectum.—(Pl. I A; Pl. II D, E)   The tectum of the male is larger and more robust than the tectum of the female.   In both sexes it is highly ornamented.   It is rectangular in shape, with its long axis running from the anterior to the posterior end of the body of the mite.   The following description is for the tectum of the male.   On its mid-ventral surface is a long, narrow, sculptured region from which radiate narrow, vein-like grooves, much like the vein pattern of a leaf.   The regions of the tectum between the ends of the veinlets and the lateral margins of the tectum appear extremely membranous and fluted.   The ornamentation thus far described is restricted to the posterior two thirds of the tectum.   The anterior third is covered with short spines which occur mainly on its lateral, ventral surfaces.   Its distal, lateral margins are dentate, but, the intervening, middle portion is smooth and curves slightly posteriorly.   The ornamentation of the tectum of the female is the same as that just given for the male except for the anterior third of the tectum.   In the female the ventral surface in this region is more completely and evenly covered with spines.   In fact they are so dense that the tectum appears very "hairy."   The middle portion of its distal margin is not curved posteriorly as is that of the male but is slightly elevated and resembles a hump.

Epipharynx.—(Pl. I F-H; II A, C)   The epipharynx of *U. agitans* is a short, broad structure, diamond in shape and supported posteriorly on a circular base.   Its ventrolateral sides are more heavily sclerotized than its dorsolateral sides.   They are distinctly corrugated and at their dorsal edges have from three to four rows of sharp teeth.   Its ventral edge extends a little beyond the base of the epipharynx.   The dorsolateral walls of the epipharynx are lightly sclerotized and look almost membranous.   They lack teeth but have numerous grooves and ridges.   These sides extend beyond the distal tip of the ventrolateral sides and terminate in a fine point.   Attached at the base of the dorsolateral sides of the epipharynx is the labrum.

Labrum.—(Pl. II A, C)   The labrum is a lightly sclerotized, spoon-shaped structure.   Its entire edge is fimbriated.

Hypopharynx.—(Pl. I F-H; II H)   The hypopharyngeal region of *U. agitans* is very well developed.   Its walls are heavily sclerotized, deeply grooved, corrugated and densely covered with small spines.   Distally, the membranous portions are thrown into a series of folds which envelope the epipharynx.   The markings of the hypopharyngeal walls correspond to those on the ventrolateral sides of the epipharynx.   Dilator muscles which originate from the ventral walls of the hypostome insert along the hypopharyngeal walls.   The hypopharynx of
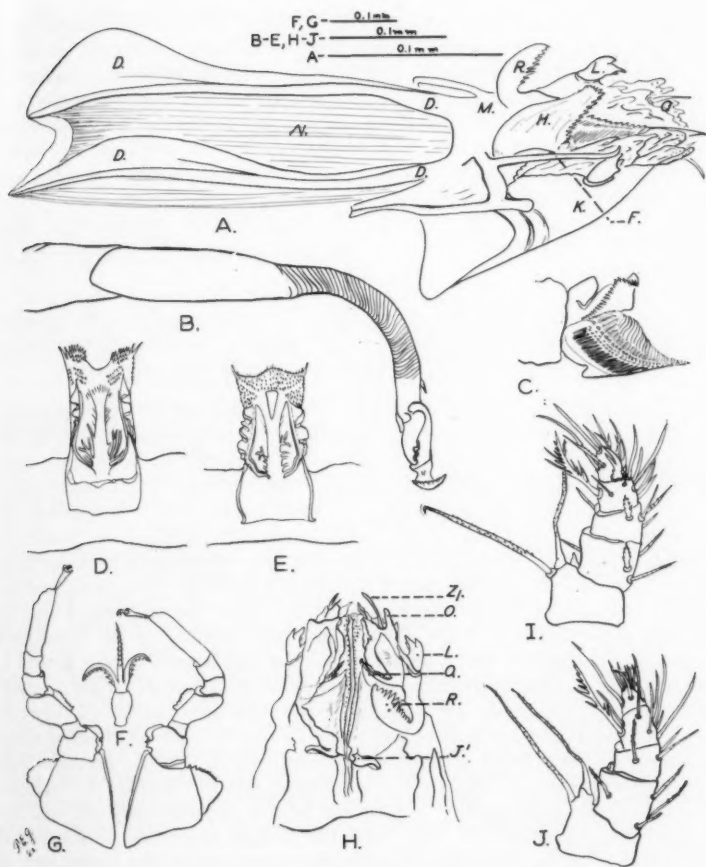
PLATE II

Legend same as for Plate I. A. Dorsolateral view of gnathosoma of female with dorsal portion of gnathosomal ring and tectum removed; B. Chelicerae; C. Epipharynx and labrum; D. Tectum of male; E. Tectum of female; F. Tritosternum; G. First pair of legs; H. Dorsal view of gnathosoma of female with dorsal portion of the gnathosomal ring, tectum, chelicerae, epistome, labrum and epipharynx removed; I. Medial view of palp; J. Lateral view of palp.

U. agitans differs sharply from the hypopharynx of *M. floridanus* in which the ornamentation is restricted to the dorsal edge of the hypopharyngeal walls.

Hypopharyngeal processes.—(Pl. I I, K; II A, H)   The long, well defined hypopharyngeal processes in *M. floridanus* are lacking as such in *U. agitans*.   They are probably represented by the numerous folds which envelop the epipharynx distally.

Hypopharyngeal styli.—(Pl. I F; II A, H)   The hypopharyngeal styli are blade-like structures which originate from the walls of the hypopharynx at the junction of the hypopharynx with the hypostome.   When the epipharynx is within the hypopharyngeal groove, the smooth, ventral surfaces of the styli rest along the proximal portion of the dorsolateral surfaces of the epipharynx. The dorsal surfaces of the styli have about fourteen teeth, the longest of which are located near the distal end of the styli.   The specific function of these styli is not known but one might suppose from their position between the chelicerae that if the epipharynx were elevated by contraction of the epipharyngeal muscles, the styli would move to a lateral position and impede the protraction of the chelicerae.

Hypostome.—(Pl. I I, K)   More than half of the anterior, ventral portion of the gnathosoma of *U. agitans* is the hypostomal region.   Except for the three pairs of hypostomal setae, the hypostome is void of ornamentation.

Hypostomal setae.—(Pl. I I, K)   The distribution of the hypostomal setae of *U. agitans* differs from the distribution of the hypostomal setae of *M. floridanus*.   In *M. floridanus* they are so arranged that by connecting their setal bases, each seta occupies a corner of a right triangle, the hypotenuse of which connects the bases of the distal and the medial setae.   If the bases of the hypostomal setae of *U. agitans* were connected a straight line would be formed with its axis running parallel with the anteroposterior axis of the body of the mite.   At the anterior end of the line would be the distal seta, and the "medial" seta would be at the posterior end.   The "lateral" seta would be approximately one third of the distance from the "medial" to the distal seta. The length of the hypostomal setae in the males and females differs as well as the numbers and the distribution of the setules on the setae.   The "medial" pair of setae in both sexes is the longest of the hypostomal setae.   In the male it is 70 microns long and has approximately 20 setules evenly distributed along its length.   In the female it measures 120 microns.   It also has approximately 20 setules but these are restricted to the proximal half of the seta.   In the male and the female the "lateral" hypostomal seta is approximately 40 microns long.   There are, however, about twice the number of setules on the lateral setae of the female (approximately 20) than there are on the lateral seta of the male.   The distal pair of hypostomal setae are the same in the male and female.   They are lateral to the hypostomal processes and resemble long, rigid spines instead of setae.   They are 30 microns long and have no setules.

Protosternum.—(Pl. I I, K)   The protosternum is anterior to the deutosternum.   It is trapezoidal in shape and its long axis (92 microns) is parallel with the long axis of the body of the mite.   It is narrower (10 microns) proximally and gradually widens (40 microns) at its distal end.   The walls are lightly sclerotized and have numerous spines scattered over their surfaces. Unlike the protosternal region of *M. floridanus*, the protosternum of *U. agitans* is apparently composed of two sclerotized plates which have fused along their medial surfaces.   At the anterior region there is some evidence that the fusing is not complete so that the protosternum in this region is split.   The exact nature of the protosternum, of course, cannot be determined until studies are made of the embryological development of *U. agitans*.

The hypostomal processes.—(Pl. II I, K) The hypostomal processes are long, slender structures which extend ventrally from the distal ends of the ventral walls of the hypostome. Their dorsal surfaces are smooth but along the ventral surface is a thin, narrow excrescence with fimbriated edges. The hypostomal processes of the female measure approximately 62 microns and those of the male approximately 55 microns.

Corniculi.—(Pl. I G-I, K) The corniculi articulate with the distal surface of the dorsolateral walls of the hypostome. They are short, stout structures, approximately 35 microns tall in the female and 30 microns tall in the male. Their distal surface is tridentated.

Chelicerae.—(Pl. I B-F; II B) The three segmented chelicerae of *U. agitans* are extremely long, slender structures which reach deep into the opisthosomal region of the body of the mite. The second segment, in which the lengthening has occurred, is not morphologically the same along its length. The posterior portion is smooth and of about the same diameter as the first segment of the chelicera. The anterior portion is narrower in diameter and is provided with numerous thickenings of the exoskeleton. Just anterior to the junction of the ribbed and the smooth portion of the segment, the segment in fixed preparations curves to the side. Whether or not this ribbed portion of the segment is capable of any flexibility has not been determined. The segment terminates in a digit, which in the female has four teeth and in the male has three. Its appearance suggests that some movement is possible, and if so it is quite different from most mesostigmatid mites in which the digit is fixed. From the distal surface of the digit extends an umbrella-shaped excrescence with fringed edges. Posterior to the digit and just anterior to the ribbed portion of the segment is a short seta. It is not consistently present in both sexes nor is it always on both chelicerae of the same specimen. The movable digit, which articulates with the digit of the second segment, has three teeth in both sexes. It is the smallest of the cheliceral segments and has no ornamentation. The extrinsic muscles of the chelicerae are short compared to the length of the chelicerae. They insert within the basal segment of the chelicerae and originate from the dorsal plate in the opisthosomal region of the body of the mite.

Pedipalps.—(Pl. II I-J) The second pair of acarine appendages, the pedipalps, are composed of six segments: the coxa, trochanter, femur, genu, tibia and tarsus. The coxae, as in all the acarina, form the greater part of the gnathosomal ring. The trochanter or first movable segment of the pedipalps is the thickest of the segments. Its ventral, anterior surface protrudes beyond the proximal portion of the segment, and from this expanded portion extend two, long, filamentous setae. The trochanters press closely against the lateral surfaces of the gnathosoma and the setae resemble slender, movable tentacles. They are of subequal length and are covered with whorls of tiny setules from their tips to about one tenth of the distance from their bases. The femur is the longest of the segments and has five setae: two lateral, two dorsal and one medial. The medial seta is the smallest of the five. It is flat and its sides are serrated. The remaining four all have small setules; the dorsal setae are the largest and of about the same length, while the two lateral setae are shorter than the dorsal setae and longer than the medial seta. The genu also has five

setae: two lateral, two dorsal and one medial. The medial is shorter than the corresponding seta of the femur. Its sides are also serrated. The two dorsal setae are shorter than the lateral setae and possess no setules. The lateral setae, one of which is more ventral than the other, are subequal in length. Both have setules. The tibia has approximately thirteen setae, mainly concentrated along its dorsal surface. Projecting from the medial, ventral surface of the tibia and directed anteriorly is a very conspicuous, robust seta. There are from two to four barbs on the proximal, dorsal portion of the seta, and on its distal, ventral portion there are from six to eight additional barbs. The remaining setae are devoid of setules and are distributed as follows: one ventral, two lateral, two medial, and seven dorsal. The ventral seta is anterior to the robust seta and about three fourths as long; the two lateral setae are slender and among the longest on the tibia; the medial setae are the shortest; three of the dorsal setae are on the anterior portion of the segment and are all long and slender; the remaining four dorsal setae are posterior, two are relatively short and stout, one curves anteriorly at about a $70°$ angle and one is the longest of the setae on the tibia. The tarsus is characterized by a two tined seta on its medial surface. Also on the medial surface is a long, straight seta, one surface of which is serrated. On its ventral surface are two setae, the most posterior of which is long, slender and curved. It extends beyond the tip of the robust seta of the tibia. The most anterior one is about half as long as the posterior seta. There is also one seta on the lateral surface of the tarsus which curves posteriorly. Along the distal, dorsal surface of the tarsus are approximately thirteen setae, all of which are nude. About eight of these, all subequal and very slender, are arranged in a circle. The remaining setae along the dorsal surface are slightly longer than these and also slender.

Salivary styli.—(Pl. I F-H; II A) The salivary styli are slender, hollow processes (about 77 microns long) which originate from the tentorial portion of the horizontal shelf and project just ventral to the tectum. At their bases open the ducts from the salivary glands. The glands are well developed organs which extend into the propodosomal portion of the body of the mite. Each gland lies on either side of the subcheliceral plate. No glands or styli were found in *M. floridanus*.

DISCUSSION

The gnathosoma of *U. agitans* is protected. Over its ventral surface project the coxae of the first pair of legs and over its dorsal surface are heavily sclerotized extensions of the dorsal plate. The skeleton of the gnathosoma is strongly sclerotized, nevertheless, although greatly reduced in size. The arrangement and construction of its parts are all adapted to accommodate the long chelicerae which in *U. agitans* are the important structures concerned with feeding. They are about one half of the length of the idiosoma and can be retracted far into the posterior region of the idiosoma; when they are protracted they extend considerably beyond the distal end of the body of the mite. In addition to the chelicerae the other structures which show evidence of greatest modification are the subchelicerae plate and the hypopharyngeal styli. To accommodate the long chelicerae the bars of the subcheliceral plate have broad, flat surfaces which tilt laterally within the body of the mite. They protrude

into the metapodosomal region.   The hypopharyngeal styli, which in *M. flori-danus* are long, lightly sclerotized, slender structures, in *U. agitans* are heavily sclerotized, blade-like structures with a deeply dentated, dorsal surface.   In *M. floridanus* they project over the dorsal surface of the epipharynx and their long axis is parallel with the long axis of the body of the mite.   In *U. agitans* they also project over the dorsal surface of the epipharynx but their long axis is perpendicular with the long axis of the body of the mite.   Their distal portions thus occur between the chelicerae.   When the walls of the hypopharynx spread and the epipharynx is raised the styli move to a lateral position and impede any further protraction of the chelicerae.   Perhaps the teeth on the dorsal walls of the styli clean the chelicerae as they are being retracted.   The corniculi of *U. agitans* are comparable in position to those of *M. floridanus*.   They too play an important role in guiding the movements of the chelicerae.   One other feature of the gnathosoma of *U. agitans* which is worthy of note from the viewpoint of function and its reflection in structure is the relatively small size of the base of the gnathosoma.   In *M. floridanus* the gnathosoma projects freely from the anterior-ventral surface of the idiosoma of the mite.   It is able to move in all directions without any difficulty.   The region occupied by the gnathosomal base comprises more than one half of the entire gnathosoma.   In *U. agitans* the entire gnathosoma is not involved in securing food.   The gnathosomal base comprises about one third of the entire gnathosoma.   It is sufficiently large to serve its principal function of providing support for the chelicerae and the pharyngeal dilator muscles.

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Two New Species of Entocythere (Ostracoda: Cytheridae), Commensal on Pacifastacus gambelii (Girard)

Eugene N. Kozloff

Lewis and Clark College, Portland, Oregon

Up to the present time, two species of *Entocythere* have been described from western crayfishes. Both of these, *E. columbia* Dobbin (1941) and *E. occidentalis* Kozloff and Whitman (1954), have been found on crayfishes referable to *Pacifastacus leniusculus* (Dana), *P. trowbridgii* (Stimpson), and *P. klamathensis* (Stimpson). Through the courtesy of Dr. R. C. Erickson, I have received a series of nine specimens of *Pacifastacus gambelii* (Girard) collected by him in a spring near the OO Ranch corral, Malheur National Wildlife Refuge, Harney County, Oregon. Examination of this material, preserved in isopropyl alcohol, disclosed the presence of two new species of *Entocythere*, for which I propose the names *Entocythere caudata* and *Entocythere ericksoni*.

The ostracods which had not fallen from the host when the latter were preserved were found primarily among the cuticular hairs on the ventral side of the thorax. A few were taken from the mouth parts. All of the host crayfish in the series I examined were populated by both species of *Entocythere*, although more individuals of *E. ericksoni* than *E. caudata* were recovered from the series as a whole.

For permanent preparations the specimens were dehydrated in ethyl alcohol, cleared in toluol, and mounted in Harleco synthetic resin.

Entocythere caudata sp. nov.

Figs. 1-12

Male.—The valves of the shell (fig. 1) are rather evenly rounded along the dorsal margin. The anterior end is acutely rounded. At the posterior end there is a distinctive tail-like projection. The ventral margin is nearly straight, but shows a slight concavity near the center, and also just in front of the posterior projection. The height of the shell is greatest near the beginning of the posterior one-third of the body. In five copulating males taken at the type locality the length of the shell ranged from about .35 mm to about .39 mm; the height ranged from about .16 mm to about .18 mm. A number of fine setae are scattered over the outside surface of each valve, principally close to the margins. The median eye is situated dorsally near the end of the first one-fifth of the body. It is heavily pigmented, and its outline, in lateral view, is oval.

The antennules (fig. 4) are composed of six podomeres. The first podomere is the longest, and the third is the shortest. The other podomeres are approximately the same length. There is one seta on the first podomere and one on the second, two setae on the third, six on the fourth, none on the fifth, and five terminal setae on the last podomere.

The antennae (fig. 5) are composed of four podomeres, the third of which is divided. A long flagellum-like exopodite originates from the basal podomere. The second podomere

bears one seta. The proximal division of the third podomere bears two setae of approximately equal length. The distal division also has two setae, one of which is a short bristle. Three terminal claws arise from the short fourth podomere. The ventral claw is the longest, and its distal half bears a number of comb-like teeth. The distal half of the dorsal claw is flattened and has approximately fourteen teeth. The short middle claw also has about fourteen teeth.

The protopodite of the mandible (fig. 8) ends in six teeth. The large anterior tooth has five cusps, while the remaining five teeth all appear to have three cusps. The convex surface of the protopodite bears a single seta. The distal podomere of the mandibular palp is sharply demarcated, but the larger, proximal part of the palp shows no trace of segmentation except for a slight irregularity in the outline of the extensor surface. There is a slender seta on the flexor side of this undivided basal podomere. Near its distal end, on the extensor side, there is one long seta. Close to this seta, and lateral to it, there is a short seta. The distal podomere bears a heavy, spine-like seta and two short bristles.

The protopodite of the maxilla (fig. 9) bears two long setae. The palp is unsegmented, and terminates in two curved setae, the more ventral of which is relatively heavy and dorsoventrally flattened.

The three pairs of thoracic legs are similar, although the legs of each successive pair are slightly longer than those of the preceding pair. Each leg is composed of four podomeres. The anterodistal corner of the first podomere of the first leg (fig. 10) bears two setae, one of which is about twice as long as the other. There is only one seta in the corresponding position on the second and third legs. The second podomere bears a single seta. There is a short, minutely hirsute seta on the third podomere. The terminal claw appears to have seven teeth.

The terminology used in describing the parts of the copulatory complex (fig. 11) is that employed by Hoff (1944). The basal piece consists of a broad proximal portion from which the clasping apparatus and ventral and dorsal fingers originate, and a more narrow distal portion. The distal portion is trough-like and truncate at the tip, with the corners drawn out into short, spine-like extensions. The clasping apparatus (fig. 12) is more or less falciform, but with rather straight vertical and horizontal rami. About half of its total length extends beyond the end of the basal piece. The tip of the clasping apparatus curves slightly upward and is divided into three teeth. There are three teeth of approximately equal size on the inner border of the distal one-third of the clasping apparatus. The dorsal finger of the copulatory complex is about half as long as the ventral finger, but the spines at the tips of the two fingers are approximately the same length.

Female.—In gravid females, the anterior end of the shell (fig. 2) is more broadly rounded than in the male. The shells of nine gravid females collected at the type locality ranged in length from about .37 mm to about .45 mm, and in height from about .18 mm to about .22 mm.

The valves of the shell in copulating females (fig. 3), resemble those of gravid females. The three copulating females collected at the type locality ranged in length from about .32 mm to about .38 mm, and in height from about .13 mm to about .16 mm.

The antennules of the gravid female are similar to those of the male, but the antennae of the two sexes are different in that the dorsal claw of the antennae of the gravid female (fig. 6) tapers gradually from its base, instead of having the distal half sharply differentiated from the proximal half.

The maxillae and mandibles of the gravid female are like those of the male. The thoracic legs of the female are also similar to those of the male, although the two setae on the first podomere of the first leg are nearly equal in length.

In copulating females, the penultimate podomere of the antenna (fig. 7) is undivided, and bears a single seta, which corresponds to one of the two setae originating from the distal division of the fourth podomere in gravid females. There are only two terminal claws on the antenna of copulating females. Otherwise the appendages of copulating females are similar to those of gravid females.

Type specimens.—The holotype (male), allotype (gravid female), and paratypes (copulating pair, gravid female), taken from *Pacifastacus gambelii* (Girard) collected by Dr. R. C. Erickson, in a spring near the OO Ranch corral, Malheur National Wildlife Refuge, Harney county, Oregon, August 15, 1952, have been deposited in the United States Museum (U.S.N.M. Nos. 95682 to 95685).

Remarks.—Of the species of *Entocythere* which have been described up to the present time, *E. caudata* is the only one in which the posterior end of the valves of the shell is drawn out into a sharp projection. The shell of *E. columbia* Dobbin has a posterior projection, but in this species it is very broad and blunt. The truncate tip of the basal piece of the copulatory complex of the male of *E. caudata* is also distinctive.
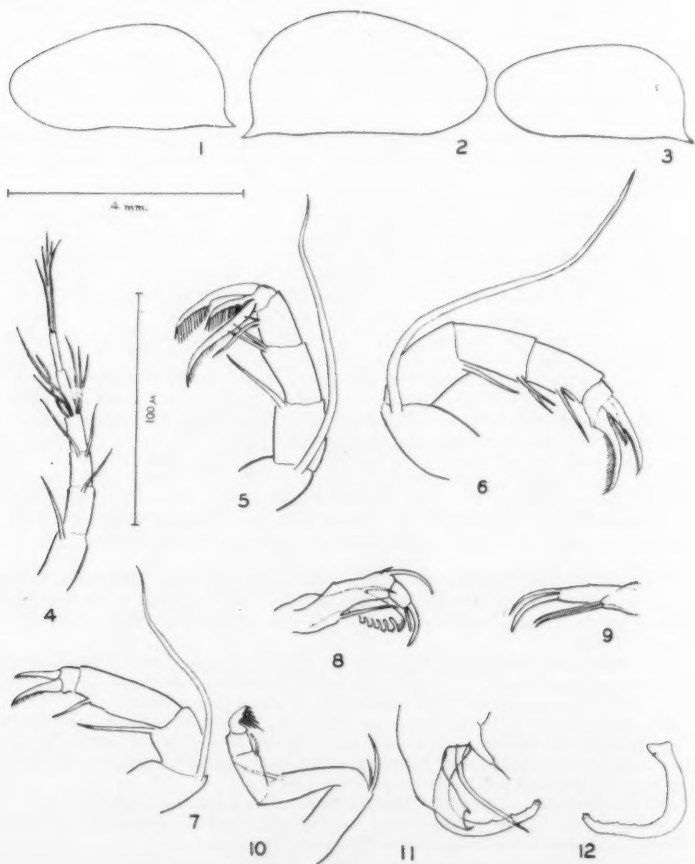
Figs. 1-12. *Entocythere caudata* sp. nov.—1-3. Outlines of valves. 1. Left of male; 2. Right of gravid female; 3. Left of copulating female; 4. Medial view of right antennule of male; 5-7. Lateral views of antennae. 5. Left of male; 6. Right of gravid female; 7. Left of copulating female; 8. Lateral view of right mandible (proximal portion omitted) of male; 9. Medial view of right maxilla (proximal portion omitted) of male; 10. Lateral view of left first thoracic leg of male; 11. Medial view of left copulatory complex of male; 12. Clasping apparatus of male. (All figures were prepared with the aid of a camera lucida. Figs. 1-3 are drawn to the scale which accompanies fig. 1; all others are drawn to the scale which accompanies fig. 4).

Entocythere ericksoni sp. nov.
Figs. 13-24

Male.—The dorsal, anterior, and posterior margins of the valves of the shell (fig. 13) are smoothly rounded. The ventral margin is markedly convex except for a slight concavity near the anterior end. The height of the shell is greatest a short distance posterior to the middle. In twenty-three copulating males taken at the type locality the length of the shell ranged from about .36 mm to about .39 mm, and the height ranged from about .19 mm to about .21 mm. There are a number of fine setae scattered on the outside surface of the valves. The median eye is heavily pigmented and situated dorsally near the end of the first one-fifth of the body. In lateral view its outline is oval.

The antennules (fig. 16) are composed of six podomeres. The first podomere is the longest and the third is the shortest. The other four podomeres are approximately the same length. There is one seta on the first podomere and one on the second, two setae on the third, six on the fourth, none on the fifth, and five terminal setae on the last podomere.

The antennae (fig. 17) are composed of four podomeres, the third of which is divided. The basal podomere has a long flagellum-like expodite. The second podomere has one seta. The proximal division of the third podomere bears two setae of approximately equal length, and the distal division bears a single seta. There are three terminal claws on the small fourth podomere. The ventral claw is the longest, and its distal half is provided with about fifteen comb-like teeth. The distal half of the dorsal claw is flattened and bears approximately fifteen teeth. The short middle claw is also toothed.

The protopodite of the mandible (fig. 18) ends in six teeth. The large anterior tooth has five cusps. Each of the remaining five teeth appears to have three cusps. The convex surface of the protopodite bears a single seta. The distal podomere of the mandibular palp is sharply demarcated, but the rest of the palp is not segmented. There is a long seta on the flexor side of the undivided basal portion. There are two setae close to the distal end of the basal portion; one of them is on the extensor side, the other is lateral and somewhat proximal to the first. The distal podomere bears a heavy spine-like seta and two short bristles.

The protopodite of the maxilla (fig. 19) bears two long setae. The palp is not segmented and terminates in two curved setae, the more ventral one being relatively stout and dorsoventrally flattened.

The three pairs of thoracic legs are similar, with the legs of each successive pair being slightly longer than those of the preceding pair. Each leg (fig. 20) is composed of four podomeres. There are two setae, one of which is about twice as long as the other, arising from the first podomere of the first leg. On the second and third legs there is a single seta in this position. There is one seta on the second podomere, and a short, minutely hirsute seta on the third podomere. The terminal claw has five teeth.

The basal piece of the copulatory complex (fig. 23) has an incision at its distal end, and the edges on either side of the incision are drawn out into short spine-like extensions. The horizontal ramus of the clasping apparatus (fig. 24) is longer than its vertical ramus. About one-half of the total length of the clasping apparatus extends beyond the end of the basal piece. Its tip is divided into five teeth. There are three teeth of approximately equal size on the inner border of the distal half of the clasping apparatus. The middle tooth is slightly nearer to the more proximal of the three teeth than to the more distal one. The dorsal finger of the copulatory complex is a little more than twice as long as the ventral finger, but the spines at the tips of the two fingers are of approximately equal length.

Female.—The concavity in the ventral margin of the valves of the shell of the gravid female (fig. 14) is more pronounced than in the male, and the height of the shell is greatest near the beginning of its posterior one-third. In 31 gravid females taken at the type locality, the length of the shell ranged from about .43 mm to about .47 mm, and the height ranged from about .23 mm to about .28 mm.

In copulating females, the ventral margin of the valves of the shell (fig. 15) is nearly straight, with only a suggestion of the concavity which is well-marked in gravid females. In eight copulating females taken at the type locality, the length ranged from about .31 mm to about .39 mm, and the height ranged from about .16 mm to about .22 mm.

The antennules of the gravid female are similar to those of the male. The antennae of the two sexes are different in that the dorsal claw of the antenna of the gravid female

(fig. 17) tapers gradually from its base, instead of having the distal half sharply differentiated from the proximal half.

The mandibles and maxillae of the gravid female are like those of the male. The thoracic legs of the female also resemble those of the male, but the two setae on the first podomere of the first leg are of approximately equal length.

In copulating females, the penultimate podomere of the antenna (fig. 18) is undivided, but has two setae which correspond to the two arising from the proximal division of this
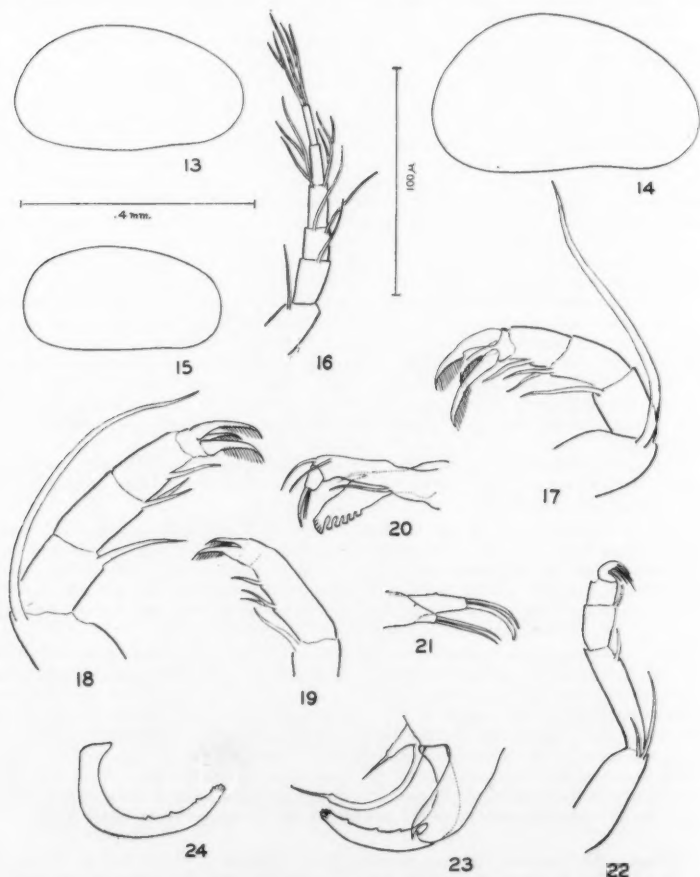
Figs. 13-24. *Entocythere ericksoni* sp. nov.—13-15. Outlines of right valves. 13. Male; 14. Gravid female; 15. Copulating female; 16. Medial view of right antennule of male; 17-19. Lateral views of antennae. 17. Left of male; 18. Right of gravid female; 19. Left of copulating female; 20. Lateral view of left mandible (proximal portion omitted) of male; 21-23. Medial views. 21. Left maxilla (proximal portion omitted) of male; 22. Right first thoracic leg of male; 23. Right copulatory complex of male; 24. Clasping apparatus of male. (All figures were prepared with the aid of a camera lucida. Figs. 13-15 are drawn to the scale which accompanies fig. 13; all others are drawn to the scale which accompanies fig. 16.)

podomere in the gravid female, and a single seta which corresponds to the one arising from the distal division of the podomere in the gravid female. There are only two terminal claws on the antenna of the copulating female. The other appendages of the copulating female are similar to those of the gravid female.

Type specimens.—The holotype (male) allotype (gravid female), and paratypes (copulating pair, gravid female) have been deposited in the United States National Museum (U.S.N.M. Nos. 95686 to 95689). These were taken from *Pacifastacus gambelii* (Girard) collected in a spring near the OO Ranch corral, Malheur National Wildlife Refuge, Harney County, Oregon by Dr. R. C. Erickson, August 15, 1952.

Remarks.—The general outline of the shell of *Entocythere ericksoni* and the presence in this species of an incision at the distal end of the basal piece of the copulatory complex, suggests a close relationship to *E. occidentalis* Kozloff and Whitman. However, the form of the clasping apparatus of *E. ericksoni* is more nearly similar to that of *E. dobbini* Rioja (1943), in that it is not C-shaped, and the vertical ramus is shorter than the horizontal ramus. *E. ericksoni* has three relatively small and more or less equal teeth in the inner border of the clasping apparatus as does the typical form of *E. dobbini*. In all the males of *E. ericksoni* which I examined, there were five teeth at the distal end of this appendage. *E. dobbini* usually has two teeth at the end of the clasping apparatus, although Rioja (1945) noted as many as four in some specimens.

SUMMARY

Entocythere caudata sp. nov. and *Entocythere ericksoni* sp. nov., commensal on *Pacifastacus gambelii* (Girard), are described from southeastern Oregon.

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A Catalogue of the Protozoa and Helminths of North American Rodents. III. Nematoda

David J. Doran*

Animal Disease and Parasite Research Branch; Agricultural Research Center, Beltsville, Maryland

This is the third of four papers summarizing the host and geographical distribution records of the protozoa and helminths reported from North American rodents (order Rodentia). The organization and limitations of this part of the catalogue are the same as those outlined in Part I (Protozoa and Acanthocephala).

NEMATODA

1. *Angiostrongylus ondatrae* (Shul'ts, Orlov, and Kutass, 1933) Dougherty, 1946.—*Ondatra zibethica* ssp. (49).

2. *Ascaris columnaris* Leidy, 1856.—*Citellus beecheyi* ssp.—Calif. (100); *Sciurus niger rufiventer*—Ill. (180).

3. *A. laevis* Leidy, 1856.—*Citellus parryi barrowensis*—Alas. (182) (142); *Marmota monax* ssp.—Pa. (35) (182); *M. m. monax [Arctomys monax* (97)]; *M. caligata broweri*—Alas. (133).

4. *A. lumbricoides* Linnaeus, 1758.—*Ondatra zibethica* ssp.—Ill. (183); *Sciurus* sp.—Ind. (182); *S. c. carolinensis*—Ohio (89); *S. niger rufiventer*—Ill. (182).

5. *A. tarbagan* Shul'ts, 1931.—*Marmota monax ochracea*—Alas. (131).

6. *A. sp.—Citellus obsoletus* (?)—Colo. (75); *Ondatra zibethica* ssp.—Nebr. (8); *Sciurus niger rufiventer*—Ohio and/or Wisc. (146); Kan. (71) (192); *Tamiasciurus hudsonicus* ssp.—Ohio and/or Wisc. (146).

7. *A.* sp. (*lumbricoides* ?).—*Ondatra zibethica* ssp.—Ill. (183); *Sciurus niger rufiventer*—Ill. (16).

8. *Ascarops* sp.—*Sciurus hudsonicus* ssp.—Tenn. (149).

9. *Aspiculuris americana* Erickson, 1938.—*Peromyscus leucopus noveboracensis*—Minn. (62); *P. maniculatus gracilis*—Minn. (62).

10. *A. tetraptera* (Nitzsch, 1821) Shul'ts, 1924.—*Mus musculus*—Minn (61); *M. m.* "albus" (175) (See Nos. 116, 117, 176).

11. *A.* sp.—*Mus musculus*—Wisc. (147).

12. *A.* sp. (*americana* ?).—*Peromyscus maniculatus gracilis*—Minn. (61).

13. *Bohmiella wilsoni* Lucker, 1943.—*Neotoma floridana osagensis*—Okla. (116); *Sciurus carolinensis* ssp.—SE U. S. (102); *S. c. leucotus*—Wisc. (146), W. Va. (102); *S. niger niger*—Va., W. Va., (102); *S. n. rufiventer*—Wisc., Minn. (146).

14. *Capillaria americana* Read, 1949 [previously reported as *Capillaria* sp. by (146) from *Glaucomys v. volans*].—*Glaucomys v. volans*—Wisc. (148), Ohio and/or Wisc. (146); *Peromyscus leucopus noveboracensis*—Ohio and/or Wisc. (148); *P. maniculatus bairdii*—Wisc. (148); *Sciurus carolinensis leucotus*—Wisc. (148).

15. *C. chandleri* Read, 1949 [previously reported as *Capillaria* sp. by (146) from *Citellus franklinii*].—*Citellus franklinii*—Wisc. (146) (148).

16. *C. hepatica* (Bancroft, 1893) Baylis, 1931.—*Castor canadensis canadensis*—D.C. *(38); *Citellus richardsonii* ssp.—Mont. (105), Alba. (15); *Mus musculus*—Md. (105); *Ondatra zibethica* ssp.—Mich. (2); *O. z. rivalica*—La. (128); *O. z. zibethica*—Maine (109); *Rattus norvegicus*—Md. (103), Ont. (64), N. Y. (82), N. C. (78); *Sigmodon hispidus* ssp.—Texas (148) (See Nos. 64, 187, 191).

17. *C. michiganensis* Read, 1949.—*Ondatra zibethica* ssp.—Mich. (148).

18. *C. muris-sylvatica* (Diesing, 1851) Travassos, 1915.—*Microtus p. pennsylvanicus*—Wisc. (147) (148).

19. *C. plica* (Rudolphi, 1819) Railliet, 1915.—*Rattus norvegicus*—Mass. (137).

20. *C. ransomia* Barker and Noyes, 1915.—*Ondatra zibethica* ssp.—Mich. (2), Ohio (141); *O. z. zibethica [Fiber zibethicus*—Minn. or Nebr. (7)].

21. *C. tamiastriati* Read, 1949 [previously reported as *Capillaria* sp. by (146) from *Tamias striatus* ssp.].—*Tamias striatus* ssp.—Wis. (148), Ohio and/or Wisc. (146).

22. *C.* sp.—*Clethrionomys rutilus dawsoni*—Alas. (144); *Rattus norvegicus*—Wisc. (157); *Sciurus c. carolinensis*—Ohio (89); *S. c. leucotus*—Ohio and/or Wisc. (146); *S. niger rufiventer*—Ohio (10) (89); *Tamias striatus* ssp.—Mass. (137) (See Nos. 65, 188).

23. *Castorstrongylus castoris* Chapin, 1925.—*Castor* sp.—Pa. (115), Colo. (126); *C. canadensis* ssp.—Minn. (63), Colo. (126), Pa. *(25), D. C. (37). (See Nos. 152, 169).

24. *Citellina triradiata* (Hall, 1916) Manter, 1930. (See No. 118).

25. *C. marmotae* Manter, 1930.—*Marmota monax* ssp.—Mich., Minn. (146); *M. m. canadensis*—Maine (106); *M. m. monax*—N. Y. (119).

26. *Citellinema bifurcatum* Hall, 1916.—*Citellus armatus*—Wyo., Idaho (54); *C. franklinii*—Man. (167); *C. richardsonii* ssp.—Man. (147) [*Citellus elegans*—Colo. (75), Wyo. (54)];

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* This work was started at the University of California, Los Angeles.

Eutamias minimus jacksoni—Minn. (146); *Glaucomys sabrinus macrotis*—Mich. (54), No. Cent. States (146); *G. volans volans*—No. Cent. States (146); *Marmota monax* ssp.—No. Cent. States (146); *M. m. rufescens*—N. Y. (54); *Sciurus c. carolinensis*—Ohio (89), Tenn. (149); *S. c. hypophaeus*—Minn. (146); *S. c. leucotus*—No. Cent. States (146); *S. hudsonicus* ssp.—Minn (54); *S. niger neglectus*—Md. (54); *S. n. rufiventer*—Ohio (10) (89), No. Cent. States (146); *Tamias striatus* ssp.—(54); *Tamiasciurus h. hudsonicus*—Man. (146); *T. hudsonicus* ssp.—No. Cent. States (146) (See Nos. 29, 30, 213).

27. *C. columbianum* Dikmans, 1938.—*Citellus columbianus* ssp.—Idaho (54).

28. *C. quadrivatti* (Hall, 1916) Manter, 1930.—(See No. 214).

29. *C. sleggsi* Manter, 1930 [=*Citellinema bifurcatum* Hall, 1916 (54)].—*Marmota monax monax*—Tenn. (149); *Sciurus c. carolinensis*—Tenn. (149) (See Nos. 26, 30, 213).

30. *C. monacis* Manter, 1930 [=*Citellinema bifurcatum* Hall, 1916 (54)].—*Marmota monax canadensis*—Maine (106) (See Nos. 26, 29, 213).

31. *Citellinoides zapodis* Dikmans, 1939.—*Napeozapus insignis* ssp.—N. C. (55).

32. *Crenosoma* sp.—*Ondatra z. zibethica*—N. Y. (69).

33. *C.* sp. (*striatum* or *taega* ?).—*Castor canadensis* ssp.—N. Y. (69).

34. *Dictyocaulus viviparus* (Bloch, 1782) Railliet and Henry, 1907.—*Microtus p. pennsylvanicus*—Mich. (147).

35. *Dipetalonema arbuta* Highby, 1943.—*Erethizon dorsatum* ssp.—Minn. (84).

36. *D. diacantha* (Molin, 1858) York and Maplestone, 1926 [=*Molinema diacantha* (Molin, 1858) Teixeira de Freitas and Lent, 1939].—*Erethizon dorsatum* ssp.—Minn. (88), Pa. *(25); *E. d. dorsatum*—Pa. *(24) (See No. 96).

37. *Dirofilaria acutiuscula* (Molin, 1858) Chitwood, 1933. (See Nos. 38, 40, 41, 42, 43).

38. *D. hystrix* Canavan, 1929 [=*D. spinosa* Canavan, 1929 (99); =*D. subdermata* (Monnig, 1924) (3)].—*Erethizon dorsatum* ssp.—Pa.* (24) (See Nos. 37, 40, 41, 42, 43).

39. *D. immitis* (Leidy, 1856) Railliet and Henry, 1911.—*Ondatra z. zibethica*—N. Y. (68); *Ondatra zibethica* ssp.—Md. (96), N. Y. (17).

40. *D. repens* Railliet and Henry, 1911 [=*D. spinosa* Canavan, 1929 (99); =*D. acutiuscula* (Molin, 1858) (38); =*D. subdermata* (Monnig, 1924) (3)].—*Erethizon dorsatum* ssp.—Pa. *(25) (See Nos. 37, 38, 41, 42, 43).

41. *D. spinosa* Canavan, 1929 [=*D. hystrix* Canavan, 1929—(24); =*D. subdermata* (Monnig, 1924) (3)].—*Erethizon dorsatum* ssp.—Minn. (83) (88); *E. d. dorsatum*—Pa. *(24) (See Nos. 37, 38, 40, 41, 42, 43).

42. *D. subcutanea* (Linstow, 1899) Canavan, 1929 [=*D. hystrix* Canavan, 1929 (24); =*D. subdermata* (Monnig, 1924) (3)]—*Erethizon dorsatum* ssp.—Pa. *(25). (See Nos. 37, 38, 40, 41, 42, 43).

43. *D. subdermata* (Monnig, 1924) Canavan, 1929.—(See Nos. 37, 38, 40, 41, 42).

44. *D.* sp.—*Erethizon d. dorsatum*—Maine. (48).

45. *D.* sp. (*immitis* ?).—*Ondatra zibethica macrodon*—Md. (166).

46. *Enterobius sciuri* Cameron, 1932.—*Glaucomys v. volans*—Ohio, Mich., Wisc. (146); *Sciurus niger rufiventer*—Ohio, Mich., Wisc. (146).

47. *Filaria obtusa* (Froelich, 1791) Schneider, 1866 [=*Protospirura muris* (Gmelin, 1790) Seurat, 1915 (75) (161); =("?") *Mastophorus muris* var. *muris* (Gmelin, 1790) Chitwood, 1938].—*Rattus norvegicus* [*Mus decumans*—D. C. (172)]. (See Nos. 85, 87, 136, 137, 138, 155.)

48. "filamentous worm" [=*Gongylonema* sp. (75)].—*Castor* sp.—Mich. (114); *C. canadensis* ssp.—Mich. (114) (See No. 55).

49. *Filaria* sp. of Morgan, 1868 [=*Setaria* sp. (75)].—*Castor* sp.—Mich. (114) (See No. 153).

50. *F.* sp.—*Castor canadensis canadensis*—Mich. (75); *Erethizon dorsatum* ssp.—Pa. *(139); *Ondatra z. zibethica* [*Fiber zibethicus*—Nebr. (70)].

51. *F.* "n. sp." (no later reference in which species is named).—*Citellus richardsonii* ssp.—Alba. (15).

52. "filarid."—*Erethizon d. dorsatum*—N. H. (91), Pa. *(67).

53. *Ganguleterakis spumosa* (Schneider, 1866) Lane, 1917 [=*Heterakis spumosa* Schneider, 1866 (107)].—*Rattus norvegicus*—D. C. (135), Ohio (65) (See No. 66).

54. *Gongylonema neoplasticum* (Fibiger and Ditlevsen, 1914) Ransom and Hall, 1916.—*Rattus norvegicus*—D. C. (101) (135).

55. *G.* sp.—*Ondatra z. zibethica*—Maine (109); *Peromyscus maniculatus osgoodi*—Colo. (74); *Sigmodon h. hispidus*—Fla. (108) (See No. 48).

56. *Heligmodendrium hassalli* (Price, 1928) Travassos, 1937.—*Sciurus c. carolinensis*—Ohio (89), Texas (31); *S. c. leucotus*—Wisc. (146); *S. niger bryanti*—Md. (57); *S. n. rufiventer*—Ohio (89), Wisc. (146), Kan. (91) (192), Texas (31); *Tamiasciurus hudsonicus* ssp.—Wisc. (146) (See Nos. 62, 79).

57. *Heligmosomum costellatum* (Dujardin, 1845) Railliet and Henry, 1909.—*Microtus montanus nanus*—Wyo. (93); *M. richardsonii macropus*—Wyo. (93).

58. *H. hudsonius* Cameron, 1937.—*Dicrostonyx groenlandicus rubricatus*—Alas. (144); *D. hudsonius*—Que., N. W. Terr. (22).

59. *H. muris* Yokogawa, 1920 [=*Nippostrongylus muris* (Yokogawa, 1920) Lane, 1923; =*Nippostrongylus brasiliensis* (Travassos, 1914) Travassos and Darriba, 1929 (188)].—*Rattus norvegicus* [*Epimys norvegicus*—Md. (207)] (See Nos. 109, 110).

60. *H. vexillatum* Hall, 1916 [=*Longistriata vexillata* (Hall, 1916) Travassos and Darriba, 1929 (188)].—*Rattus norvegicus*—Colo. (75); *Thomomys fossor*—Colo. (75) (See No. 83).

61. *H.* sp.—*Sciurus niger bryanti*—Md. (57).

62. *Heligmostrongylus hassalli* Price, 1928 [=*Heligmodendrium hassalli* (Price, 1928) Travassos, 1937].—*Sciurus carolinensis* ssp.—Md. (133) (See Nos. 56, 79).

63. *Hepaticola gastrica* Baylis, 1926 [=*Capillaria gastrica* (Baylis, 1926) (11)].—*Rattus norvegicus*—D. C. (1).

64. *H. hepatica* (Bancroft, 1893) Hall, 1916 [=*Capillaria hepatica* (Bancroft, 1893) Travassos, 1915 (11)].—*Cynomys ludovicianus*—Pa.* (21); *Mus musculus*—Pa.* (205); *Ondatra zibethica* ssp.—Ont. (94) (134); *Rattus norvegicus*—D. C. (46) (135), Pa. *(204) [*Epimys*

norvegicus—Md. (207), Pa., D. C., R. I., Calif. (75); [*Epimys rattus norvegicus*—Md. (163)]; *Thomomys fossor*—Wyo. (51) (See Nos. 16, 187, 191).

65. *H.* sp. [=*Capillaria* sp. (11)].—*Cynomys* sp.—Pa. *(138); *C. ludovicianus* ssp.—Pa. *(140); *Marmota monax monax* [*Arctomys monax* ssp.—Pa. *(138)]. (See Nos. 22, 188).

66. *Heterakis spumosa* Schneider, 1866 [=*Ganguletrakis spumosa* (Schneider, 1866) Lane, 1917 (197)].—*Mus musculus*—N. C. (78); *Rattus norvegicus*—Md. (103), N. Y. (82), N. C. (78), Wisc. (157), Ont. (64), Mex. (209) [*Epimys norvegicus*—Md. (204) (207), D. C., Mass., Ohio, Nebr., Mich., Okla. (75); *Mus norvegicus*—Pa. (24), Wisc., (110); *Rattus r. norvegicus*—Mex. (19)]; *R. rattus* [*Epimys rattus*—D. C., Md., Mass., Ohio, Nebr., Mich., Okla., (75)]; "rat" (*R. norvegicus* ?)—Miss. (199) (See No. 53).

67. *H.* sp.—*Rattus norvegicus* [*Mus decumans*—Mass., D. C., (172)].

68. *Heteroxynema cucullatum* Hall, 1916.—*Eutamias minimus operarius* [*Eutamias amoenus operarius*—Colo. (75).

69. *Impalaia* sp.—*Sciurus carolinensis* ssp.—Ill. (16); *S. niger rufiventer*—Ill. (16).

70. *Kalicephalus simplex* (Leidy, 1856) Walton, 1927.—(See Nos. 168, 197).

71. *Litomosoides carinii* (Travassos, 1919) Vaz, 1934.—*Sigmodon hispidus* ssp.—Texas (58), SW U. S. (12); *S. h. texianus*—Texas (160); *S. h. littoralis*—Fla. (202); *S. melanotis*—Mex. (209); *Ondatra zibethica* ssp.—Texas (30) (See Nos. 72, 73, 95, 212).

72. *L. pattersoni* (Mazza, 1928) Chitwood, 1933.—(See Nos. 71, 73, 95, 212).

73. *L. sigmodontis* Chandler, 1931 [=*L. pattersoni* (Mazza, 1928) (39); =*L. carinii* (Travassos, 1919) Vaz, 1934 (193)].—*Sigmodon hispidus* ssp.—Texas (26) (See Nos. 71, 72, 95, 212).

74. *L.* sp.—*Neotoma micropus* ssp.—Texas (58).

75. *Longistriata adunca* Chandler, 1932.—*Ondatra zibethica rivalica*—La. (128); *Sigmodon* sp.—Texas (159); *S. hispidus* ssp.—SW. U. S. (12), Texas (28); *S. h. hispidus*—N. C. (79) (80), Texas (86).

76. *L. carolinensis* Dikmans, 1935.—*Microtus ochrogaster*—Ind. (52); *Peromyscus maniculatus* ssp.—N. C. (52); *P. m. nebracensis*—Ind. (52).

77. *L. convoluta* Caballero and Zerecero, 1943.—*Crateogeomys merriami*—Mex. (20).

78. *L. dalrymplei* Dikmans, 1935.—*Microtus pennsylvanicus* ssp.—Ind. (52); *M. p. pennsylvanicus*—Wisc. (147), Va., Minn. (52); *Ondatra zibethica* ssp.—Ind., Miss (52), Texas (30).

79. *L. hassalli* (Price, 1928) Dikmans, 1935 [=*Heligmodendrium hassalli* (Price, 1928) Travassos, 1937 (188)].—*Sciurus c. carolinensis*—N. C. (78) (See Nos. 56, 62).

80. *L. musculi* Dikmans, 1935 [("?") reported as *Longistriata* sp. by (158)].—*Mus musculus*—La. (52).

81. *L. neotomae* Murphy, 1952.—*Neotoma floridana osagensis*—Okla. (116).

82. *L. norvegica* Dikmans, 1935.—*Rattus* sp.—La. (52)

83. *L. vexillata* (Hall, 1916) Travassos and Darriba, 1929.—(See No. 60).

84. *Mastophorus muris* var. *ascaroides* (Hall, 1916) Chitwood, 1938.—*Geomys* sp.—Fla. (85); *G. breviceps* ssp.—Okla. (42); *Oryzomys palustris* ssp.—Ga. (42); *Peromyscus leucopus* ssp.—Va. (42); *Thomomys fossor*—Colo. (42); *Sigmodon hispidus* ssp.—N. C. (79); *S. h. hispidus*—Texas (86), Ga., N. C. (80) (See Nos. 86, 134, 135).

85. *M. muris* var. *muris* (Gmelin, 1790) Chitwood, 1938.—*Rattus norvegicus*—D. C. (42) [*R. rattus norvegicus*—Texas (86)]; *R. n.* "albus"—(42); *Sigmodon hispidus hispidus*—Texas (86) (See Nos. 47, 87, 136, 137, 138, 155).

86. *M. muris* (Gmelin, 1790) Chitwood, 1938 [("?") =*M. muris* var. *ascaroides* (Hall, 1916)].—*Clethrionomys* sp.—Alas. (144); *Microtus* sp.—Alas. (144); *M. p. pennsylvanicus*—Mich. (147). (See Nos. 84, 134, 135).

87. *M. muris* (Gmelin, 1790) Chitwood, 1938 [("?") =*M. muris* var. *muris* (Gmelin, 1790)].—*Rattus norvegicus*—Can. (64) (See Nos. 47, 85, 136, 137, 138, 155).

88. *Mecistocirrus* sp.—*Sciurus carolinensis* ssp.—!ll. (16).

89. *Microfilaria alpha* Chandler, 1942.—*Sciurus niger rufiventer*—Texas (31).

90. *M. beta* Chandler, 1942.—*Sciurus niger rufiventer*—Texas (31).

91. *M. rosenaui* McCoy, 1911.—*Citellus beecheyi* ssp.—Calif. (100) (120).

92. *M.* sp.—*Erethizon dorsatum*—Maine (48).

93. "microfilaria."—*Citellus mexicanus*—Texas (58); *Neotoma a. albigula*—Ariz. (206); *N. a. melanura*—Mex. (206); *N. micropus* ssp.—Texas (58); *Perognathus penicillatus pricei*—Mex. (206); *Peromyscus leucopus* ssp.—Texas (58); *Rattus norvegicus*—Mex. (14); *Sigmodon hispidus* ssp.—Texas (58).

94. "microfilaria" (*Dipetalonema* sp. or *Dirofilaria* sp.).—*Erethizon dorsatum* ssp.—Minn. (88).

95. *Micropleura sigmodoni* Ochoterena and Caballero, 1932 [=*Vestibulosetaria pattersoni* (Mazza, 1928) Vogel and Gabaldon, 1932 (194); =*Litomosoides carinii* (Travassos, 1919) Vaz, 1934 (193)].—*Sigmodon hispidus* ssp.—Mex. (125) (See No. 53).

96. *Molinema diacantha* (Molin, 1858) Teixeira de Freitas and Lent, 1939.—*Erethizon dorsatum dorsatum*—Maine (48) (See No. 36).

97. *Monodontus floridanus* McIntosh, 1935.—*Sigmodon hispidus* ssp.—Fla. (121).

98. *Nematodirus neotoma* Hall, 1916 [previously reported as *Nematodirus* sp. by (74)].—*Neotoma desertorum*—Colo. (74); *N. cinerea rupicola*—Colo. (74) [*Neotoma rupicola*—U. S. (187)]; *N. floridana baileyi*—Colo. (74) [*Neotoma baileyi*—U. S. (187)]; *N. mexicana fallax*—Colo. (74) [*Neotoma fallax*—U. S. (187)].

99. *N.* sp.—*Eutamias quadrivittati*—Colo. (74).

100. *N. tortuosus* Tucker, 1942.—*Neotoma fuscipes macrotis*—Calif. (190); *N. lepida intermedia*—Calif. (190).

101. *Nematospira turgida* Walton, 1923.—*Microtus pennsylvanicus* ssp. (196).

102. *Nematospiroides aberrans* (Roe, 1929) Travassos, 1937.—(See Nos. 104, 154).

103. *N. carolinensis* Dikmans, 1940—*Clethrionomys gapperi* ssp.—N. C. (56).

104. *N. dubius* Baylis, 1926.—*Mus musculus*—Calif. (170) (See Nos. 102, 154).

105. *N. longispicularis* Dikmans, 1940.—*Microtus longicaudus littoralis*—Alas. (144); *M. pennsylvanicus* ssp.—Md. (56); *Ondatra zibethica* ssp.—N. J. (56).

106. *N. microti* Kuns and Rausch, 1950.—*Microtus montanus nanus*—Wyo. (93); *M. richardsonii macropus*—Wyo. (93).

107. *N.* sp.—*Lemmus trimucronatus alacensis*—Alas. (144); *Microtus p. pennsylvanicus*—Wisc., Minn. (147).

108. *N.* sp. (*microti* ?).—*Microtus richardsonii macropus*—Wyo. (93).

109. *Nippostrongylus brasiliensis* (Travassos, 1914) Travassos and Darriba, 1929—(See Nos. 59, 110).

110. *N. muris* (Yokogawa, 1920) Lane, 1923 [=*N. brasiliensis* (Travassos, 1914 (188)].—*Mus musculus*—Md. (9); *Rattus norvegicus*—Md. (103) (168), Ohio (65), Ind. (21), Wisc. (157), N. C. (78), Texas (27), Ont. (64) [*Epimys norvegicus*—Texas (29); *Epimys rattus norvegicus*—Md. (72); *Mus norvegicus*—Pa. (24)] (See Nos. 59, 109).

111. "nematode."—*Citellus tridecemlineatus pallidus*—Colo. (74) (75); *C. richardsonii* [*Citellus elegans*—Colo. (74)]; *Dipodomys merriami merriami*—N. Mex., Ariz. (111); *Marmota monax rufescens*—N. Y. (76); *Sciurus c. carolinensis*—Texas (70); *Tamias striatus lysteri*—N. H. (132); *Thomomys fossor*—Colo. (74).

112. "nematode" (larval).—*Peromyscus l. leucopus*—N. C. (78).

113. *Obeliscoides cuniculi* (Graybill, 1923) Graybill, 1924.—*Marmota monax* ssp.—Ohio, Mich. (146) (145), Minn. (195); *M. m. monax*—Mo. (191).

114. *Ollulanus tricuspis* Leuckart, 1865 (larval).—*Mus musculus*—D. C. (75).

115. *Oxyuris evoluta* Linstow, 1899 [=*Wellcomia evoluta* (Linstow, 1899) (208); =*W. evaginata* (Linstow, 1899) (107) (127)].—*Erethizon dorsatum* ssp.—(165), Wisc., Pa.*, D. C.* (75); *E. epixanthum* ssp.—Wisc., Pa.*, D. C.* (75) (See Nos. 215, 216).

116. *O. obvelata* (Rudolphi, 1802) Dujardin, 1845 [=*Aspiculuris tetraptera* (Nitzsch, 1821) Shul'ts, 1924, in part (169); =*Syphacia obvelata* (Rudolphi, 1802) Seurat, 1916 (75) (161) (208)].—*Clethrionomys g. gapperi* [*Evotomys rutilus*—U. S. (75)]; *Erethizon dorsatum* ssp.—Pa. (165); *Mus musculus*—Colo. (74); *M. m.* "albus"—(75); *Neotoma mexicana fallax* —Colo. (75); *Onychomys leucogaster* ssp.—Colo. (75); *Peromyscus nasutus*—U. S. (75); *R. rattus* [*Epimys rattus*—U. S. (75)]; *R. norvegicus* [*Mus decumans*—D. C. (172)] (See Nos. 10, 117, 176).

117. *O. tetraptera* (Nitzsch, 1821) Linstow, 1878 [=*Aspiculuris tetraptera* (Nitzsch, 1821) —(169)].—*Mus musculus*—Colo., D. C. (75) (See Nos. 10, 116, 176).

118. *O. triradiata* Hall, 1916 [=*Citellina triradiata* (Hall, 1916) Manter, 1930].—*Citellus leucurus cinnamomeus* [*Ammospermophilus leucurus cinnamomeus*—Colo. (75)]; *C. l. leucurus* [*Ammospermophilus l. leucurus*—U. S. (75)]; *C. lateralis* ssp. [*Callospermophilus lateralis* ssp.—Colo. (75)] (See No. 24).

119. *O.* sp.—*Eutamias minimus operarius* [*Eutamias amoenus operarius*—Colo. (74)]; *E. quadrivittatus*—Colo. (74); *Microtus mordax* ssp.—Colo. (74); *M. p. pennsylvanicus* [*Arvicola riparus*—Md. (172)]; *Neotoma cinerea rupicola*—Colo. (74); *N. floridana baileyi*—Colo. (74); *Pitymys pinetorum pinetorum* [*Arvicola pinetorum*—Md. (172)]; *Sciurus niger bryanti*—Md. (57).

120. "oxyurids."—*Erethizon dosatum* ssp.—Pa.* (138); *Marmota monax* ssp.—Minn. (146).

121. *Passalurus ambiguus* (Rudolphi, 1819) Dujardin, 1845.—*Marmota* sp.—N. Y. (5).

122. *P. abditus* Caballero, 1937.—*Citellus variegatus variegatus* [*Otospermophilus variegatus*—Mex. (8)].

123. *Physaloptera bispiculata* Vaz and Pereira, 1935 [=*Physaloptera getula* Seurat, 1917 (113)].—*Cynomys ludovicianus*—Mont., Colo. (111); *Ondatra zibethica rivalica* [*Ondatra rivalica*—La. (111)]; *Sigmodon hispidus* ssp.—Fla., Ga., Texas (111) (See No. 124).

124. *P. getula* Seurat, 1917. (See No. 123).

125. *P. hispida* Schell, 1950.—*Sigmodon hispidus littoralis*—Fla. (155).

126. *P. massino* Shul'ts, 1926 [previously reported as *Physaloptera* sp. by (112)].—*Sciurus niger niger*—Wisc. (113) (See Nos. 128, 130).

127. *P. muris-brasiliensis* Diesing, 1861.—*Rattus norvegicus*—Iowa (113); *Sigmodon hispidus* sp.—Ga. (112); *S. h. hispidus*—Ga. (113).

128. *P. spinicauda* McLeod, 1933 [=*P. massino* Shul'ts, 1926 (112)].—*Citellus franklinii* —Can. (122); *C. tridecemlineatus* ssp.—Man. (122) (See Nos. 126, 130).

129. *P.* sp.—*Citellus franklinii*—Wisc. (146); *C. richardsonii* ssp.—Alba. (15); *C. t. tridecemlineatus*—Wisc., Minn. (146); *Ondatra zibethica rivalica*—La. (128); *Sciurus carolinensis leucotus*—Wisc. (146).

130. *P.* sp. (*bispiculata* ?) of Baylis, 1935 [=*P.* sp. (*massino* ?) (113)].—*Sigmodon hispidus* ssp.—SW U. S. (12) (See Nos. 126, 128).

131. *Physocephalus sexalatus* (Molin, 1860) Diesing, 1861.—*Sigmodon h. hispidus*—Fla. (108).

132. "pinworms."—*Sciurus c. carolinensis*—Texas (70).

133. *Protospirura anodon* Hannum, 1943 [previously reported (in part) as *Protospirura* sp. by (4)].—*Onychomys torridus* ssp.—Ariz. (77); *Perognathus penicillatus pricei*—Ariz. (77).

134. *P. ascaroidea* Hall. 1916 [=("?") *Mastophorus muris* var. *ascaroides* (Hall, 1916) Chitwood, 1938].—*Geomys b. breviceps*—Texas (60); *Sigmodon hispidus texianus*—Okla. (36) (See Nos. 84, 86, 135).

135. *P. ascaroidea* Hall. 1916 [=*M. muris* var. *ascaroides* (Hall, 1916) Chitwood, 1938]. —*Geomys breviceps* ssp.—Okla. (75) (See Nos. 84, 86, 134).

136. *P. columbianum* Cram. 1926 [=*M. muris* var. *muris* (Gmelin, 1790) Chitwood, 1938 (42)]—*Rattus norvegicus*—D. C. (45) (See Nos. 47, 85, 87, 137, 138, 155).

137. *P. muris* (Gmelin. 1790) Seurat. 1915 [=*M. muris* var. *muris* (Gmelin, 1790) Chitwood, 1938].—*Mus musculus*—Colo. (75); *Rattus norvegicus* [*Ebimys norvegicus*—Colo. (75)]; *R. rattus* [*Epimys rattus*—U. S. (75)] (See Nos. 47, 85, 87, 136, 138, 155).

138. *P. muris* (Gmelin. 1790) Seurat. 1915 [=("?") *M. muris* var. *muris* (Gmelin, 1790) Chitwood, 1938].—*Mus musculus*—Ill. (92); *Rattus norvegicus* [*Mus norvegicus*—Pa. (24)]; *R. n.* "albus"—(46) (See Nos. 47, 85, 87, 136, 137, 155).

139. *P. numidica* Seurat, 1914.—*Peromyscus g. gossypinus*—Ga. (42); *P. g. megacephalus* —Tenn. (42).

140. *P. tetradon* Hannum, 1943 [previously reported (in part) as *Protospirura* sp. by (4)].—*Perognathus penicillatus pricei*—Ariz. (77).

141. *Ransomus rodentorum* Hall, 1916 [previously reported as *Chabertia* sp. by (74)].—*Thomomys fossor*—Colo. (75).

142. *Rictularia citelli* McLeod, 1933.—*Citellus franklinii*—Can. (122); *C. tridecemlineatus* ssp.—Man. (122); *C. t. tridecemlineatus*—Wisc. Minn. (146) (See No. 145)

143. *R. coloradensis* Hall, 1916.—*Eutamias amoenus* ssp.—Wash. (136); *E. quadrivittatus* ssp.—Colo. (75); *Microtus longicaudus* ssp.—Wash. (136); *Peromyscus l. leucopus*—N. C. (78); *P. maniculatus* ssp.—Wash. (136); *P. m. bairdii*—Wisc. (178).

144. *R. dipodomis* Tiner, 1948.—*Dipodomys* sp. (*merriami* ?)—Ariz. (179).

145. *R. halli* Sandground, 1935 [=*R. citelli* McLeod, 1933 (178)].—*Eutamias* (=*Tamias*)[1] *striatus lysteri*—Mich. (154); *Sciurus carolinensis leucotus*—Wisc. (146); *Tamias striatus* ssp.—Wisc. (146); *T. s. griseus*—Wisc. (178) (See No. 142).

146. *R. microti* McPherson and Tiner, 1952 [previously reported as *Rictularia* sp. by (144)].—*Microtus oeconomus inniutus*—Alas. (123);*M. miurus paneaki*—Alas. (123) (144).

147. *R. ondatrae* Chandler, 1941.—*Ondatra zibethica* ssp.—Texas (30); *Oryzomys p. palustris*—S. C. (178); *Sigmodon hispidus texianus*—Texas (108).

148. *R. onychomis* Cuckler, 1939.—*Onychomys leucogaster* ssp.—Nebr. (47); *Peromyscus leucopus* ssp.—Tenn. (149), Pa. (35); *Sciurus niger* ssp.—Ohio (81).

149. *R. sp.*—*Clethrionomys rutilus dawsoni*—Alas. (144); *Eutamias minimus jacksoni*—Minn. (146); *Peromyscus leucopus noveboracensis*—W. Va. (203); *Sciurus niger rufiventer*—Ohio (10); *Tamiastriatus hudsonicus* ssp.—Ohio (146); *Neotoma magister*—Ind. (123).

150. *R. sp.* (*coloradensis* ?).—*Sciurus c. carolinensis*—Ohio (89); *S. niger rufiventer*—Ohio (146) (89), Kan. (71) (192).

151. *R. sp.* (*ondatrae* ?).—*Ondatra zibethica rivalica*—La. (128).

152. *Sclerostoma* sp. of Morgan, 1868 [=*Strongylus* sp. (75); =*Castorstrongylus castoris* Chapin, 1925 (63)].—*Castor* sp.—Mich. (114) (See Nos. 23, 169).

153. *Setaria* sp.—(See No. 49).

154. *Sincosta aberrans* Roe, 1929 [=*Nematospiroides aberrans* (Roe, 1929) Travassos, 1937; =*Nematospiroides dubius* Baylis, 1926 (30) (56)].—"wild mouse"—N. J. (151) (See Nos. 102, 104).

155. *Spiroptera obtusa* (Froelich, 1791) Rudolphi, 1809 [=*Protospirura muris* (Gmelin, 1790) Seurat, 1915 (75) (161); =("?") *Mastophorus muris* var. *muris* (Gmelin, 790) Chitwood, 1938].—*Mus musculus*—Colo. (74) (See Nos. 47, 85, 87, 136, 137, 138).

156. *S. sp.*—*Citellus tridecemlineatus pallidus*—Colo. (74); *Cynomys ludovicianus*—Colo. (74).

157. *Spirura infundibuliformis* McLeod, 1933.—*Citellus richardsonii* ssp.—Man. (122); *C. tridecemlineatus* ssp.—Man. (122); *C. t. tridecemlineatus*—Minn. (146).

158. *S. michiganensis* Sandground, 1935.—*Eutamias* (=*Tamias*)[2] *striatus lysteri*—Mich. (154); *Tamias striatus* ssp.—Wisc. (146).

159. *S. sp.* (*infundibuliformis* ?).—*Citellus richardsonii* ssp.—Alas. (15).

160. *Spiruracerca zapi* Erickson, 1938.—*Zapus h. hudsonius*—Minn. (62).

161. *S. sp.* (*zapi* ?).—*Zapus h. hudsonius*—Minn. (61).

162. *Strongyloides papillosus* (Wedl, 1856) Ransom, 1911.—*Rattus norvegicus* [*Epimys norvegicus*—U. S. (75) Md. (207)]; *Sciurus c. carolinensis*—Tenn. (149).

163. *S. ratti* Sandground, 1925.—*Rattus norvegicus*—Md. (103) (153), N. J. (73), Mo. (189), Ont. (64) [*Epimys rattus norvegicus*—Md. (162)].

164. *S. ratti* var. *ondatrae* Chandler, 1941.—*Ondatra zibethica* ssp.—Texas (30).

165. *S. robustus* Chandler, 1942.—*Sciurus c. carolinensis*—Texas (31); *S. niger bryanti*—Md. (57): *S. n. rufiventer*—Texas (31).

166. *S. sigmodontis* Melvin and Chandler, 1950.—*Sigmodon* sp.—Texas (159); *S. hispidus hispidus*—Fla. (108); *S. h. texianus*—Texas (108).

167. *S. sp.*—*Sciurus carolinensis* ssp.—(43); *S. c. leucotus*—Mich. and/or Wisc. (146); *S. niger rufiventer*—Mich. and/or Wisc. (146); *Sigmodon hispidus* ssp.—SW U. S. (12); *Tamiasciurus hudsonius* ssp.—Mich. and/or Wisc. (146).

168. *Strongylus simplex* Leidy, 1856 [=*Kalicephalus simplex* (Leidy, 1856) Walton, 1927; =*Trichostrongylus* (s. l.) *simplex* (Leidy, 1856) Travassos, 1918 (188)].—*Erethizon d. dorsatum* [*Hystrix dorsata* (97) (172)] (See Nos. 70, 197).

169. *S. sp.*—*Rattus norvegicus* [*Mus decumanus*—Md. (172)] (See Nos. 23, 152).

170. *Subulura ungulatus* Erickson, 1938.—*Zapus h. hudsonius*—Md. (62).

171. *S. sp.*—*Citellus franklinii*—Man. (167).

172. *S. sp.* (*ungulatus* ?).—*Zapus h. hudsonius*—Minn. (61).

173. *Syphacia artica* Rausch, 1950.—*Dicrostonyx* sp.—Alas. (144); *D. groenlandicus rubricatus*—Alas. (185); *Lemmus* sp.—Alas. (144).

174. *S. citelli* Tiner and Rausch, 1950.—*Citellus armatus*—Wyo. (185).

175. *S. eutamii* Tiner, 1948 [previously reported as *Syphacia* sp. by (146)].—*Eutamias minimus* ssp.—Minn. (146) (177).

176. *S. obvelata* (Rudolphi, 1802) Seurat, 1916 [=*Oxyuris obvelata* (Rudolphi, 1802) Dujardin, 1845 (75)].—*Clethrionomys gapperi gapperi* [*Evotomys g. gapperi*—U. S. (75)]; *Eutamias amoenus* ssp.—Wash. (136); *Microtus* sp.—Alas. (144); *M. longicaudus* ssp.—Wash. (136); *M. l. mordax*—Wyo. (93); *M. mexicanus* ssp.—Mex. (143); *M. montanus* ssp.—Wash. (136); *M. m. nanus*—Wyo. (93); *M. ochrogaster*—No. Cent. States (147); *M. pennsylvanicus drummondi*—No. Cent. States (147); *M. p. modestus*—Wyo. (93); *M. p. pennsylvanicus*—No. Cent. States (147), Minn. (61); *M. richardsonii macropus*—Wyo. (92); *Mus musculus*—Minn. (61); *M. m. "albus"*—(74) (175); *Ototylomys p. phyllotis*—Mex. (41); *Peromyscus maniculatus* ssp.—Wash. (136); *Rattus norvegicus*—Md. (103),

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[1] Names of rodent genera not synonymous; members of the genus *Eutamias* do not occur in Michigan [See (43)].
[2] See footnote [1].

Ohio (65), Mo. (189), Alas. (156) [*Rattus r. norvegicus*—Texas (86)]; *R. n.* "albus" (46) (196); *R. rattus*—U. S. (75); *Reithrodontomys megalotis* ssp.—Wash. (136); "rat"—Iowa (13); "rat" (*R. norvegicus* ?)—Miss. (199) (See Nos. 10, 116, 117).

177. *S. peromysci* Harkema, 1936.—*Peromyscus l. leucopus*—N. C. (78).

178. *S. thompsoni* Price, 1928.—*Glaucomys sabrinus macrotis*—Mich., Wisc. (146); *G. volans volans*—Va. (133); *Tamiasciurus hudsonicus* ssp.—Wisc. (184).

179. *S. samorodini* Erickson, 1938.—*Peromyscus leucopus noveboracensis*—Minn. (62); *P. maniculatus gracilis*—Minn. (62).

180. *S. sp.*—*Citellus beecheyi* ssp.—Calif. (100).

181. *S. sp. (samorodini* ?).—*Peromyscus leucopus noveboracensis*—Minn. (62).

182. *Travassosius americanus* Chapin, 1925 [=*Travassosius rufus* Khalil, 1922 (23)].—*Castor sp.*—Pa. (115), Mont. (152); *C. canadensis* ssp.—D. C. (37), N. Y.* (118), Minn. (63), Colo. (126) (See No. 183).

183. *T. rufus* Khalil, 1922.—*Castor canadensis canadensis*—Can. (23) (See No. 182).

184. *Trichinella spiralis* (Owen, 1835) Railliet, 1895.—*Citellus tridecemlineatus* ssp.— Iowa (173); *Mus musculus*—U. S. (75); *M. m.* "albus" (75); *Rattus norvegicus*—Md. (103), D. C. (135), Mass. (137), Mich. (50), Ind. (21), Mo. (189), La. (130), Alas. (156) [*Epimys norvegicus*—U.S. (75) [*Mus norvegicus*—Wisc. (110); *Rattus r. norvegicus*—Calif. (90)]; *R. rattus* [*Mus rattus*—U.S. (171)]; "rat" (*R. norvegicus* ?)—Miss. (199).

185. *Trichocephalus muris* Schrank, 1788 [=*Trichuris muris* (Schrank, 1788) Hall, 1916 (169)].—*Rattus norvegicus*—Ind. (21), Mo. (189) (See No. 206).

186. *T. sp.* [=*Trichuris* sp.).—*Erethizon dorsatum* ssp.—(172) (See No. 211).

187. *Trichosoma hepaticum* (Bancroft, 1893) Railliet, 1898 [=*Hepaticola hepatica* (Bancroft, 1893) (75); =*Capillaria hepatica* (Bancroft, 1893) (11)].—*Cynomys ludovicianus*—Pa.* (200); *Geomys* sp.—Pa.* (200) (See Nos. 16, 64, 191).

188. *T. sp.* [=*Capillaria* sp. (11)].—*Rattus norvegicus* [*Mus decumans*—D. C. (172)] (See Nos. 22, 65).

189. *Trichosomoides crassicauda* (Bellingham, 1845) Railliet, 1895.—*Rattus norvegicus*— Md. (103), D. C. (135), N. C. (78). Ohio (65), Wisc. (157), Alas. (156), Ont. (64) [*Epimys norvegicus*—Md. (207), Ill. (176), U. S. (75)]; *Rattus n.* "albus" (46); *R. rattus*— U. S. (75) [*Epimys rattus*—U.' S. (75)].

190. *T. sp.* (*crassicauda* ?).—*Sigmodon h. hispidus*—Ga. (80).

191. *Trichosomum* (?) *tenuissimus* Leidy, 1890 [=*Hepaticola hepatica* (Bancroft, 1893) (75); =*Capillaria hepatica* (Bancroft, 1893) (11)].—*Rattus norvegicus* [*Mus decumans* (98)] (See Nos. 16, 64, 187).

192. *Trichostrongylus calcaratus* Ransom, 1911.—*Marmota monax monax* (53); *Ondatra zibethica* ssp.—Pa. (34) (35); *Sciurus carolinensis leucotus*—Wis. (146); *S. niger rufiventer*— Wisc. (146), Kan. (71) (192) (See No. 195).

193. *T.colubriformis* (Giles, 1892) Ransom, 1911.—(See No. 194).

194. *T. delicatus* Hall, 1916 [=*T. colubriformis* (Giles, 1892) (124)]—*Sciurus aberti nimus*—Colo. (75) (See No. 193).

195. *T. fiberius* Barker and Noyes, 1915 [=*T. calcaratus* Ransom, 1911 (34)].—*Ondatra z. zibethica* [*Fiber zibethicus*—Nebr. (7)] (See No. 192).

196. *T. sigmodontis* Baylis, 1945.—*Sigmodon hispidus* ssp.—SW U. S. (12).

197. *T. simplex* (Leidy, 1856) Travassos, 1918.—(See Nos. 70, 168).

198. *T. texianus* Dikmans, 1937.—*Cynomys ludovicianus arizonensis*—Texas (53).

199. *T. sp.*—*Marmota monax monax*—N. Y.* (119); *Ondatra zibethica occipitalis*—Ore. (150); *Sciurus carolinensis hypophaeus*—Minn. (146); *S. niger rufiventer*—Minn. (146); *Tamias striatus* ssp.—Wisc. (146).

200. *Trichuris citelli* Chandler, 1945.—*Citellus beecheyi* ssp.—Calif. (32).

201. *T. contorta* (Rudolphi, 1819) Hall, 1916.—*Neotoma albigula* ssp.—Ariz. (77).

202. *T. fossor* Hall, 1916 [previously reported as *Trichuris* sp. by (74)].—*Thomomys fossor*—Colo. (74) (75); *Thomomys b. bottae*—Calif. (32).

203. *T. leporis* (Froelich, 1789) Hall, 1916.—*Citellus richardsonii* ssp.—Man. (181) (146).

204. *T. madisonensis* Tiner, 1950 [previously reported as *Trichuris* sp. by (146)].—*Tamias striatus* ssp.—Wisc. (146) (181).

205a. *T. minuta* (Rudolphi, 1819) Chandler, 1930.—*Citellus variegatus* ssp. [*Citellus grammurus*—Ariz. (77)]; *Dipodomys merriami* ssp.—Ariz. (77); *D. ordii* ssp.—Ariz. (77); *Perognathus baileyi* ssp.—Ariz. (77); *P. flavius* ssp.—Ariz. (77); *P. intermedius* ssp.—Ariz. (77) (See No. 205b).

205b. *T. minuta* (Rudolphi, 1819) of Hannum, 1943 [previously reported as *Trichuris* sp. by (4)].—*Perognathus penicillatus pricei*—Ariz. (4) (77). (See No. 205a).

206. *T. muris* (Schrank, 1788) Hall, 1916.—*Neotoma floridana osagensis*—Okla. (116); *Rattus norvegicus*—Mex. (209) (See No. 185).

207. *T. 'neotomae* Chandler, 1945.—*Neotoma fuscipes* ssp.—Calif. (32).

208. *T. opaca* Barker and Noyes. 1915.—*Microtus p. pennsylvanicus*—Nebr. (181); *M. richardsoni macropus*—Wyo. (93); *Ondatra zibethica* ssp.—Mich. (2), Ohio (141); *O. z. cinnamominius*—Nebr. (181); *O. z. osooyoensis*—Colo. (6); *O. z. zibethica*—N. Y. (59), Wisc. (147), No. Cent. States (181) [*Fiber zibethicus*—Nebr. (7)]; *O. z. macrodon*—Md. (129).

209. *T. perognathi* Chandler, 1945.—*Perognathus c. californicus*—Calif. (32); *Perognathus penicillatus* ssp.—Ariz. (33).

210. *T. peromysci* Chandler, 1946.—*Peromyscus californicus* ssp.—Calif. (33).

211. *T. sp.*—*Microtus ochrogaster*—Ill. (147); *Thomomys monticola* ssp.—Calif. (87) (See No. 186).

212. *Vestibulosetaria pattersoni* (Mazza, 1928) Vogel and Gabaldon. 1932 [=*Litomosoides pattersoni* (Mazza, 1928) Chitwood, 1933: =*L. carinii* (Travassos, 1919) (193)].—*Sigmodon hispidus* ssp.—Mex. (194) (See Nos. 71, 72, 73, 95).

213. *Warrenius bifurcatum* Sleggs, 1925 [=*Citellinema sleggsi* Manter. 1930 (106); =*Citellinema fiburcatum* Hall, 1916 (54)].—*Citellus richardsonii* ssp.—Sask. (164) (122), Man. (122) (See Nos. 26, 29, 30).

214. *W. quadrivatti* Hall, 1916 [=*Citellinema quadrivatti* (Hall, 1916) Manter, 1930].—*Eutamias quadrivittatus* ssp.—Colo. (75) (See No. 28).

215. *Wellcomia evaginata* (Smith, 1908).—*Erethizon epixanthum*—Colo. (127) (See Nos. 115, 216).

216. *W. evoluta* (Linstow, 1899) Baylis, 1922 [=*W. evaginata* (Smith, 1908) (107) (127)].—*Erethizon dorsatum* ssp.—Minn. (88), Mass. (137), N. Y.* (117), Pa.* (25); *E. d. dorsatum*—Maine (48), N. H. (91); *E. epixanthum* ssp.—Mont. (88), Ariz. (174) (See Nos. 115, 215).

217. *W. longejector* Hannum, 1943 [previously reported as *Wellcomia* (n. sp.) by (4)].—*Dipodomys merriami* ssp.—Ariz. (77); *Perognathus baileyi* ssp.—Ariz. (77); *P. intermedius* ssp.—Ariz. (77); *P. penicillatus pricei*—Ariz. (4).

(A Host-Index to the parasite names listed herein will be found at the end of Part IV (Trematoda), which will appear in the next issue of this journal.)

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Ecology of Worm Parasites in South-central New York Salamanders*

Jacob H. Fischthal

Harpur College, Endicott, New York

During the periods from July 19-September 17, 1950 and May 25-July 8, 1951, a total of 503 salamanders from different collection points in 5 counties (Broome, Cortland, Delaware, Tioga, Tompkins) of south-central New York were examined for helminth parasites and 220 (43.7 percent) were found infected with at least one species. In 1950 284 salamanders were examined and 219 in 1951. The late May to mid-September coverage is nearly the entire active season for salamanders in this area, except for approximately a month on each end. Hosts examined were 105 newts (*Triturus v. viridescens*), 1 Jefferson's salamander (*Ambystoma jeffersonianum*), 36 red-backed salamanders (*Plethodon c. cinereus*), 25 slimy salamanders (*Plethodon g. glutinosus*), 24 purple salamanders (*Gyrinophilus p. porphyriticus*), 134 two-lined salamanders (*Eurycea b. bislineata*), and 178 dusky salamanders (*Desmognathus f. fuscus*). The variation in numbers of different host species examined is indicative of their relative abundance in the area studied. According to Bishop (1941), and personal observations in the field, *Triturus* is aquatic, while *Plethodon c. cinereus* and *P. g. glutinosus* are terrestrial; *Gyrinophilus*, *Eurycea* and *Desmognathus* are terrestro-aquatic. *Ambystoma jeffersonianum* will not be considered in the discussion in this report inasmuch as the size of the sample is wholly inadequate from which to draw any conclusions. From the hosts listed 22 different species of helminths were recovered, 10 of which were trematodes, 3 cestodes, and 9 nematodes (table 1).

In an abstract of a paper read at the 26th annual meeting of the American Society of Parasitologists, Fischthal (1951) presented a preliminary discussion of the data considered in this report.

Little has been done in the United States on the ecology of parasites in salamanders. Most earlier papers either described new species or considered the parasites in a few salamanders in connection with a more extensive study on other amphibians and on reptiles. To date, only two significant ecological studies have been published. Rankin (1937), in North Carolina, examined 1,010 salamanders for the most extensive of these parasite studies. Later, Rankin (1945), in western Massachusetts, presented the results of an examination of 209 salamanders for helminths.

Appreciation is expressed to Dr. A. C. Walton, Knox College, Galesburg, Illinois, for aid in identifying some of the nematodes listed in this paper.

TABLE 1.—The distribution of helminth parasites in the salamanders

		Triturus v. viridescens	Ambystoma jeffersonianum	Plethodon c. cinereus	Plethodon g. glutinosus	Gyrinophilus p. porphyriticus	Eurycea b. bislineata	Desmognathus f. fuscus	Totals
	Examined	105	1	36	25	24	134	178	503
	Infected	99	1	1	18	5	39	57	220
	% Inf.	94.3	100	2.8	72.0	20.8	29.1	32.0	43.7
Trematodes	No.	83	1	1	16	1	5	20	127
	%	79.0	100	2.8	64.0	4.2	3.7	11.2	25.2
	No. spp.	6¹(1)	2(1)	1	1	1	2(1)	2	10(3)
Cestodes	No.	13	0	0	0	0	29²	3	45
	%	12.4					21.6	1.7	8.9
	No. spp.	1					2(1)	1	3(1)
Nematodes	No.	65³	0	0	3	5	8	37	118
	%	61.9			12.0	20.8	6.0	20.8	23.4
	No. spp.	3(1)			1	3	1	3	9(1)

¹ No. preceding parentheses indicates total no. of spp. regardless of developmental stage;
no. within parentheses indicates no. of larval species making up total.

² No. and % high due to larval cestodes. Adults occurred only in 3 (2.2%).

³ No. and % high due to larval nematodes. Adults occurred only in 52 (49.5%).

Helminths recovered.—The figures in parentheses following the name of the host under each species of parasite represent the following: first figure—total number of individuals harboring that parasite; middle figure—percent infection; last figure—average number of worms per host. All helminths reported in this study represent new distribution records.

TREMATODA

BRACHYCOELIUM SALAMANDRAE (Froelich) Dujardin, 1845

Hosts: Triturus v. viridescens (5-4.8-2), *Plethodon c. cinereus* (1-2.8-3), *P. g. glutinosus* (16-64.0-15.5), *Gyrinophilus p. porphyriticus* (1-4.2-19), *Eurycea b. bislineata* (4-3.0-1.5), *Desmognathus f. fuscus* (13-7.3-1.6).
Position: Small intestine.

This parasite was found in more hosts than any other single species. It has a world-wide distribution and has been recorded from both amphibians and reptiles. Its occurrence in *Gyrinophilus p. porphyriticus* represents a new host record. Rankin (1938) reviewed the genus *Brachycoelium*, reducing all known species to synonymy with *B. salamandrae*. In this area the terrestrial *Plethodon g. glutinosus* appears to be the most important host for this parasite, possibly because a terrestrial invertebrate serves as intermediate host. Over 60 specimens, of which only 10 were mature, were recovered from a single host; no more than 10 mature specimens were taken from any one. Most all other hosts harbored less than 10 specimens, whether immature or mature; the 19 in *Gyrinophilus* were immature. Crowding of these worms in the intestine caused them to be smaller in size at sexual maturity.

GORGODERINA ATTENUATA Stafford, 1902

Host: *Triturus v. viridescens* (14-13.3-2.6).
Position: Urinary bladder.

The life cycle of this parasite has been reported by Rankin (1939). An aquatic environment is required, involving a macrocercous cercaria developing in finger-nail clams, a metacercaria in tadpoles, and the eating of the latter by the definitive host (amphibians and reptiles). The nature of the life cycle appears to limit this parasite to salamanders in an aquatic habitat. Crowding by several worms of this species in the bladder resulted in smaller individuals at maturity.

MEGALODISCUS TEMPERATUS (Stafford, 1905) Harwood, 1932

Host: *Triturus v. viridescens* (46-43.8-3.4).
Position: Large intestine.

Krull and Price (1932) described the life cycle of this parasite. Amphistome cercariae develop in aquatic snails; metacercariae occur on the skin of tadpoles and frogs, or if cercariae are eaten by a tadpole, they encyst in the upper digestive tract and excyst in the lower part of the intestine; those encysted on the skin get into frogs when the stratum corneum is shed and eaten. This parasite is limited to salamanders living in or occasionally entering an aquatic environment for the life cycle requires that type of habitat. Smaller sexually mature forms were obtained when crowding occurred in the large intestine.

PHYLLODISTOMUM SOLIDUM Rankin, 1937

Host: *Desmognathus f. fuscus* (7-3.9-1.4).
Position: Urinary bladder.

Goodchild (1943) reported the life cycle of this gorgoderid parasite. Macrocercous cercariae develop in finger-nail clams; encystment occurs in odonatan naiads.

Groves (1945) also obtained encystment in odonatan naiads, and in addition in aquatic larval dusky salamanders, the latter being the normal second intermediate host in the area in Ohio studied. Dusky salamanders become infected upon ingestion of the metacercarial hosts. An aquatic environment is absolutely necessary for this parasite cycle. *P. solidum* shows strict host-specificity, having been recorded almost exclusively from the terrestro-aquatic *Desmognathus fuscus*.

Although Groves (1945) did record a single specimen of *P. solidum* from one of 97 *Eurycea b. bislineata*, he stated that it probably was an accidental case of parasitism.

PLAGITURA PARVA Stunkard, 1933 and P. SALAMANDRA Holl, 1928

Host: *Triturus v. viridescens* (48-45.7-5.4).
Position: Small intestine.

Some worms were definitely identified as *P. parva* and others as *P. salamandra*. However, when many worms were crowded together within the host, they were smaller in size, reducing their apparent morphological differences. Under such conditions it was extremely difficult separating these two closely related forms. Stunkard (1936) reported the life cycle of *P. parva*, while Owen (1946) recorded it for *P. salamandra*. Both species require aquatic snails for cercarial development; metacercariae occur in snails and aquatic insect larvae; adult newts become infected by ingesting the snail or larval or adult insect. Rankin (1937) has recorded the rare occurrence of *Plagitura salamandra* in other species of salamanders.

TREMATODA, IMMATURE

Hosts: *Triturus v. viridescens* (1-0.9-6), *Ambystoma jeffersonianum* (1-100-4).
Position: Stomach.

These worms from the two different hosts appeared to be identical. From their location within the stomach and the fact that no distinctive morphological development had as yet been attained, it appears that they were recently ingested metacercariae. The worms possessed a very large acetabulum and at the anterior end a series of black granules giving the appearance of an inverted-Y (probably the digestive system).

METACERCARIAE (3 species)

Hosts: *Triturus v. viridescens* (5-4.8-15), *Ambystoma jeffersonianum* (1-100-1), *Eurycea b. bislineata* (1-0.7-1).

Positions: Kidney, liver, wall of body cavity (*Triturus*); mesentery (*Ambystoma, Eurycea*).

The metacercariae from *Triturus* were enclosed by a thick hyaline cyst. More than 60 cysts occurred in 1 specimen. Those from *Ambystoma* and *Eurycea* were within thin-walled cysts, and possessed a Y-shaped excretory bladder filled with black granules; in addition it was readily noted that metacercariae from the latter host possessed short intestinal crura ending over the acetabulum.

CESTODA

BOTHRIOCEPHALUS RARUS Thomas, 1937

Hosts: *Triturus v. viridescens* (13-12.3-3), *Eurycea b. bislineata* (3-2.2-3).
Position: Small intestine.

Thomas (1937) described the life cycle of this tapeworm from *Triturus*. Coracidia are ingested by copepods and develop into procercoids. These, when eaten by the final host, develop into adult worms. Adult *Triturus* may also become infected by eating infected larval *Triturus*. The life cycle is, therefore, confined to an aquatic habitat. Crowding of individuals in the small intestine of *Triturus* resulted in smaller tapeworms. The occurrence of this parasite in the terrestro-aquatic *Eurycea b. bislineata* represents a new host record.

CYLINDROTAENIA AMERICANA Jewell, 1916

Host: *Desmognathus f. fuscus* (3-1.7-1.7).
Position: Small intestine.

This tapeworm has been recorded from frogs by a number of investigators and from a lizard by Harwood (1932). Rankin (1937) referred to an unpublished thesis by Mann (1932) in which *C. americana* is recorded in North Carolina also from *Desmognathus f. fuscus.*

PROTEOCEPHALID CYSTS

Host: *Eurycea b. bislineata* (27-20.1-1.8).
Position: Small and large intestines, mesentery.

These larval tapeworms occurred in thin-walled, transparent cysts attached mainly to the outer lining of the small intestine; occasionally, they were attached to the outer lining of the large intestine or to the mesentery. They all possessed four rounded suckers, and a fifth apical sucker on the scolex.

NEMATODA

CAPILLARIA TENUA Mueller, 1932

Host: *Triturus v. viridescens* (51-48.6-2.3).
Position: Small and large intestines.

This nematode occurred mainly in the inner lining of the wall of the small intestine, but occasionally in a similar position in the large intestine. Rankin (1945), in Massachusetts, has reported this parasite from the above host in addition to its being occasionally found in frogs. The parasite appears confined to an aquatic habitat.

COSMOCERCOIDES DUKAE (Holl, 1928) Wilkie, 1930

Host: *Triturus v. viridescens* (6-5.7-3.3).
Position: Small and large intestines.

Those specimens from the small intestine were larvae, while immature females were taken from the large intestine. This parasite has been listed by various investigators from many species of aquatic and terrestrial amphibians and reptiles in Canada and the United States.

OXYSOMATIUM AMERICANA (Walton, 1929) Walton, 1933

Hosts: *Eurycea b. bislineata* (9-6.7-1.8), *Desmognathus f. fuscus* (4-2.2-1).

Position: Large intestine.

Larvae, immature females, and adult males and females were found in *Eurycea*, while adult males were in *Desmognathus*. The presence of this nematode in these salamanders represents new host records. Previously it had been reported from toads, frogs, spadefoot, and a salamander (*Siren lacertina*) in the United States.

OXYSOMATIUM LONGICAUDATA (Walton, 1929) Walton, 1933

Hosts: *Plethodon g. glutinosus* (3-12.0-3), *Gyrinophilus p. porphyriticus* (1-4.1-1).

Position: Small and large intestines.

Larvae and adult male and female worms occurred in the large intestine in *Plethodon*, while a single male specimen was found in the small intestine of *Gyrinophilus*. These 2 species of salamanders represent new hosts for this parasite, the latter having previously been recorded only from the frog, *Rana pipiens*, in the United States.

"OXYURIS" MAGNAVULVARIS Rankin, 1937

Host: *Desmognathus f. fuscus* (18-10.1-1.6).

Position: Large intestine.

This nematode has been reported from many species of salamanders in the United States. Its identification is based solely on the female worm, the male never having been found.

PHARYNGODON sp.

Host: *Gyrinophilus p. porphyriticus* (1-4.1-1).

Position: Small intestine.

This specimen was identified by Dr. A. C. Walton (personal communication) as an immature male of the genus *Pharyngodon*, near *bassii*. *P. bassii* Walton, 1940, was described from the intestine of *Hyla septentrionalis* in Cuba.

SPIRONOURA sp.

Host: *Gyrinophilus p. porphyriticus* (3-12.5-4.3).

Position: Small intestine.

Walton (personal communication), after reviewing the specimens stated, "The material . . . seems to have many characteristics of the genus *Spironoura*. The caudal papillae, the precloacal musculature, and the position of the vulva are characteristic, but the esophagus is atypical. The head region is very similar to that of *S. elongata*. The size of the spicules is less than has been reported earlier, but the shape and form is right, and so is the small accessory piece." *S. elongata* (Baird, 1858) Walton, 1932, was described from the intestine of the tiger salamander, *Ambystoma tigrinum* in Mexico.

(?) SPIRONOURA sp.

Host: *Desmognathus f. fuscus* (14-7.9-1.1).

Position: Cysts on wall of small intestine; adults in large intestine.

Larvae were extracted from thin-walled, transparent cysts on the outer wall of the small intestine, while adult males and females occurred in the large intestine. Walton (personal communication) wrote, "a form seemingly near *Spironoura*, but not entirely typical. I do not know this form at all."

SPIRURID CYSTS

Host: *Triturus v. viridescens* (34-32.4-3.8).

Position: Stomach and large intestine.

The cysts were embedded in the walls of the stomach in all but one host; the latter had cysts embedded only in the walls of the large intestine. Adults of this type of nematode are known to occur in reptiles; the encysted larvae are found in aquatic vertebrates.

DISCUSSION

The older and more permanent the habitat, the more parasitic species may be expected in salamanders. Older and more permanent waters with no inlet or outlet build up a higher incidence and intensity of parasitism. As illustration, *Triturus* showed a much higher incidence and intensity of infection when taken from a lake or pond than from a stream. Of the 105 specimens examined for parasites, 99 were infected. Only 8 of the 105 were from a stream, but 4 (50 percent) of these were negative; of the 97 from lakes and ponds, only 2 (2.1 percent) were negative. The stream provides a less stable, ever-changing habitat, and thus fewer species and individuals of parasites occur.

Size of the lake or pond usually makes a difference in the incidence and intensity of infection. Small areas generally tend to build up a concentration of parasites and hosts. In relation to the parasitism of *Triturus* an interesting ecological situation was noted whereby this species of salamander from a large lake showed an equally high degree of parasitism as did specimens taken from several small, isolated ponds. In large Sky Lake, Broome County, the shallow water is limited to a 5-10 foot strip along shore before the bottom drops off very suddenly. Thus the littoral zone is much reduced, concentrating the parasites and salamanders within a small area and effectively creating a close superposition of necessary conditions for a high parasitism characteristic of small ponds.

Seasonal variations in incidence and intensity of parasitism was noted. A greater degree of infection was observed in 1950 in those salamanders collected from about mid-summer on (July 19-September 17), while the reverse was true in the 1951 collections of late spring and early summer (May 25-July 8). Rankin (1937), in North Carolina, also concluded that a greater infection occurs primarily during the summer than during other seasons.

There appears to be a definite correlation between habitat preference of the salamanders and their parasitism. In table 1 it is readily seen that the aquatic *Triturus* possessed the highest incidence and number of species of parasites. From the data on the helminths recovered it is noted that, in general, this same salamander also had the greatest intensity of infection. Multiple infections were commonly found. Of the 99 infected, 28 had 1 species of parasite, 33 had 2, 26 had 3, and 12 had 4. In the terrestro-aquatic *Gyrinophilus*, *Eurycea*, and *Desmognathus* the incidence, intensity, and number of species of parasites was significantly less. Multiple infections were uncommon in these salamanders. No multiple infections occurred in *Gyrinophilus*; only 5 of the 39 infected *Eurycea* and 4 of the 57 infected *Desmognathus* had a maximum of 2 different species of parasites in the same individual. The terrestrial *Plethodon c. cinereus* and *P. g. glutinosus* showed the least number of species of parasites, and would also have the lowest incidence and intensity of infection were it not for the occurrence of a single species of trematode, *Brachycoelium salamandrae*, in *glutinosus*. Multiple infections were rare in the terrestrial hosts, none occurring in *cinereus* and only 1 with 2 species of parasites in *glutinosus*. Rankin (1937) concluded from his studies in North Carolina that "terrestro-aquatic salamanders have a variety of habitats, and, consequently, harbor more species of parasites than do others." The aquatic salamanders were more heavily parasitized than terrestrial ones. His study (1945) in Massachusetts indicated that the aquatic *Triturus v. viridescens* harbored more species of parasites than

did the terrestro-aquatic and terrestrial salamanders. In this latter paper he refers to an unpublished thesis by Little (1928) in which aquatic salamanders of North Carolina were reported more heavily infected than terrestrial species.

The greatest incidence and number of species of trematodes were recovered from the aquatic host *Triturus*. Five adult, 1 immature and 1 larval species were encountered. The terrestro-aquatic hosts showed fewer species of trematodes with 2 adult forms in *Desmognathus*, 1 adult and 1 larval in *Eurycea*, and 1 adult in *Gyrinophilus*. The 2 terrestrial species of *Plethodon* had only 1 species of trematode present. Because of the nature of the life cycle in most trematodes, involving aquatic intermediate hosts, these parasites would be expected to occur most frequently in aquatic salamanders, less so in those which only occasionally frequent water, and uncommon in terrestrial hosts whose life, following transformation from the larva, is spent almost entirely on land. Host-specificity of the trematodes for the species of salamanders herein studied would also, in part, account for the presence of a trematode in one and not in the others. Among the cestodes and nematodes, discounting larval infections, the incidence of parasitism was greatest in the aquatic *Triturus*, intermediate in the terrestro-aquatic salamanders, and low in the terrestrial forms. The number of species of adult cestodes and nematodes were approximately equal in individual aquatic and terrestro-aquatic host species; terrestrial salamanders had no cestodes and only 1 species of nematode.

The intensity of a parasitic infection in these salamanders determined, in several instances, the size of the worms present. In *Triturus* the size at maturity of the trematodes *Brachycoelium salamandrae*, *Gorgoderina attenuata*, *Megalodiscus temperatus* and *Plagitura* spp., and the cestode *Bothriocephalus rarus* were affected. The more worms of a species present in the same position of a host salamander, the smaller their size at maturity; conversely, the fewer worms present, the larger they are at maturity. Similar observations were made for *Brachycoelium salamandrae* in the other species of salamanders. Rankin (1937, 1945) noted this general condition for salamander parasites from North Carolina and Massachusetts.

SUMMARY

An ecological study conducted in 1950 and 1951 of the helminth parasites of 503 salamanders belonging to 7 species from south-central New York has been presented. Of the 503 hosts examined, 220 or 43.7 percent were infected with at least one species of parasite. Twenty-two species of helminths were encountered: 10 trematodes, 3 cestodes and 9 nematodes. Trematodes occurred in 25.2 percent of the 503 salamanders, cestodes in 8.9 percent, and nematodes in 23.4 percent. The older and more permanent the habitat, the more parasitic species were present and the greater the incidence and intensity of infection. Small lakes and ponds tend to build up a concentration of parasites and hosts, unlike larger areas. Seasonal variations in parasitism were noted, being heavier from mid-summer to fall, and lighter in late spring and early summer. The life cycles of the parasites and host-specificity played an important role in the presence of the helminths in some of the salamanders. There was a definite correlation between habitat preference of the salamanders and their parasitism, the aquatic *Triturus* having the highest incidence and number

of species of helminths; the terrestro-aquatic hosts were intermediate, while the terrestrial ones were lowest. Multiple helminth infections occurred commonly in aquatic salamanders, uncommonly in terrestro-aquatic, and rare in terrestrial. The intensity of the parasitic infection determined in several instances the size of the worms at maturity; crowding resulted in smaller worms. It is apparent that there exists a definite relationship between the habitat, the life cycle, and host-specificity.

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Studies on Fish Parasites of Lake Huron
and Manitoulin Island

Ralph V. Bangham
The College of Wooster, Wooster, Ohio

The data presented are the result of studies carried on during the summer of 1951. The survey was conducted at the fisheries laboratory of the Ontario Department of Lands and Forests at South Baymouth, Manitoulin Island.* A majority of the fish were obtained from South Bay where many fish were collected as a part of the research studies of the laboratory. Other fish were secured from nets in the open lake near South Baymouth. Fish from several of the Manitoulin Island lakes were obtained by the use of gill nets. Most of the game fish examined for parasites were secured through the cooperation of creel census workers and the line fishermen. The assistance of the laboratory staff was much appreciated in helping to secure hosts for parasite study. Special acknowledgement for aid is given to the director, Dr. Fred E. J. Fry, to John Budd and to James Fraser.

In all, a total of 1,667 fish belonging to 53 different species were examined and 1,642 or 98.5 per cent carried at least one species of parasite. This is quite a high degree of infection due possibly to the fact that most of the hosts were adults and to the high degree that fish carried the encysted metacercariae of eye flukes belonging to the genus *Diplostomulum*. In other fish parasite surveys the degree of infection has been quite varied, due to many different factors. Bangham and Hunter (1939) reported a 58.3 per cent infection as a result of a study of 2,156 Lake Erie fish belonging to 79 different species. Many were minnows and young fish. The number of parasites was less in hosts from the eastern portions of the lake.

In 1944 (*unpublished data*) the writer found 97.9 per cent of 1,811 northeastern Wisconsin fish from 50 locations to be parasitized. Bangham (1941a) reported 84.3 per cent parasitism for 560 fish belonging to 22 species from Algonquin Park lakes. Bangham and Venard (1942) report 94.9 per cent of 558 fish from Reelfoot Lake parasitized while Bangham (1951) reports 92.3 per cent of 2,351 fish belonging to 14 different species parasitized from the upper Snake River Drainage.

Most of the fish were examined while fresh or after being preserved on ice. A few were frozen and examined at a later time.

The species of fish are arranged according to the classification of Hubbs and Lagler (1947). Species of parasites are listed in order of frequency of occurrence, the number following each parasite name indicating the number of hosts harboring the form. The degree of infection and distribution are discussed in the text for each species. Encysted larval forms are indicated by a single asterisk (*), while immature stages within the digestive tract are marked by a double asterisk (**).

* South Bay Fisheries Laboratory, Division of Research, Ontario Department of Lands and Forests.

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Sea Lamprey—PETROMYZON MARINUS Linnaeus

Hosts examined 13; infected 9. Parasites: **Proteocephalus sp.—8, P. laruei—2, *Triaenophorus crassus—2,*Diplostomulum sp.—1, Echinorhynchus salmonis[1]—1.

One lamprey from Lake Huron outside of South Bay was free of parasites. One of two from the North Channel of Lake Huron carried immature Proteocephalus sp. and E. salmonis in its intestinal tract. Eight of 10 lampreys from South Bay carried the remaining listed forms.

ROCK STURGEON—ACIPENSER FULVESCENS Rafinesque

Host examined 1; infected 1. Parasites: Crepidostomum lintoni—1, Cucullanus clitellarius—1, Diplobothrium hammulatum—1, *Diplostomulum sp.—1, Echinorhynchus salmonis—1.

This was an adult host from South Bay. But few rock sturgeons have been examined for parasites by the writer. In the Lake Erie survey (Bangham and Hunter, 1939) the parasites of two sturgeons were listed. Both carried C. lintoni and C. clitellarius and one had unidentified flukes belonging to the genus Allocreadium. Bangham (unpublished data) found parasites in four rock sturgeons from Upper Lake Pepin. All carried C. lintoni, one had D. hammulatum on its gills, one had Rhabdochona cascadilla and two of these hosts carried a species of Spinitectus. A single large sturgeon from the Embarass River, Wisconsin, taken in 1944 yielded about 40 endoparasitic C. lintoni and hundreds of D. hammulatum from the gills.

Bowfin—AMIA CALVA Linnaeus

Hosts examined 3; infected 3. Parasites: *Diplostomulum sp.—3, Haplogothrium globuliforme—3, Haplonema immutatum—3, Proteocephalus perplexus—3, Leptorhynchoides thecatus—2, Macroderoides typicus—1, Pomphorhynchus bulbocolli—1.

All of these hosts were taken in South Bay. Twenty bowfins from three locations in the Upper Mississippi River (unpublished data) yielded a total of 12 different parasite species. All of those taken from South Bay hosts were recovered except the eye flukes Diplostomulum sp.

Thirteen species of parasites were found in 21 bowfins from Southern Florida (Bangham, 1941b).

American Smelt—OSMERUS MORDAX (Mitchill)

Hosts examined 50; infected 50. Parasites: Diplostomulum sp.—47, Echinorhynchus salmonis—36, *E. salmonis—16, *Spinitectus gracilis—2, *Pomphorhynchus bulbocolli—1, *Philometra sp.—1.

Ten of these smelt came from gill nets in the North Channel of Lake Huron. All of these had eye flukes and all but one carried intestinal E. salmonis. The single cyst of Philometra was recovered from one of these hosts. The remaining hosts came from South Bay nets. All of the infections were light except for 11 of the 37 with more than 10 Diplostomulum in the lenses of their eyes.

Lake Herring—LEUCICHTHYS A. ARTEDI (LeSueur)

Hosts examined 79; infected 79. Parasites: Proteocephalus laruei—71, *Triaenophorus crassus—61, *Diphyllobothrium sp.—54, *Diplostomulum sp.—48, Salmincola inermis—19, S. wisconsinsensis—11, Discocotyle salmonis—9, Proteocephalus exiguus—9, *Echinorhynchus salmonis—6, *Philometra sp.—5, Argulus sp.—4, Echinorhynchus salmonis—4, *Myxosporidia—4, Abothrium crassum—3, Cystidicola stigmatura—3.

P. laruei is a weak cestode which is a common form in the intestine of this host. It was the only parasite from four lake herrings from Bass Lake, near Espanola. T. crassus was encysted in the flesh of hosts from South Bay, Lake Huron outside South Baymouth and in two of the three hosts from the North Channel of Lake Huron. Nine of the 58 hosts from South Bay infected with T. crassus had more than 10 cysts in each fish. Dr. Richard B. Miller (1943) says, "Cestodes of the genus Triaenophorus are the most troublesome tapeworms in Canadian fishes. The plerocercoids of this genus are found in large and con-

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[1] The Acanthocephala in this study were identified by H. J. Van Cleave who is here, for the first time, recognizing Echinorhynchus coregoni Linkins as a direct synonym of E. salmonis Mueller.

spicuous cysts, frequently in muscles of valuable food fishes: these cysts often occur in great numbers." Most of the *Diphyllobothrium* cysts were near the stomach and a few were found in the muscles of the organ. All but five of the 54 infected hosts had less than 10 cysts in each lake herring.

S. inermis was taken from the gill cavities of the hosts, the tissues often being swollen and inflamed when infected with this parasitic copepod. *S. inermis* was taken from 11 of 70 South Bay hosts and one of three herrings from North Channel. The other species of this genus, *S. wisconsinensis*, was found on the body surface and fins of 11 hosts from South Bay. In five hosts, both species of these parasitic copepods were taken.

S. wisconsinensis was described from a lake herring from Trout Lake (Wisconsin) by Tidd and Bangham (1945). *D. salmonis* was first described by Elmer Schaffer in 1916 from rainbow trout at the State Hatchery, Cold Spring Harbor, New York. Later it was reported from hosts at several other fish hatcheries and from fishes at the New York Aquarium. It has been infrequently reported from fishes in open waters.

Longjaw Chub—LEUCICHTHYS ALPENAE Koelz

Host examined 1; infected 1. Parasites: *Diplostomum* sp.—1, *Echinorhynchus salmonis*—1.

This host came from the North Channel of Lake Huron.

Great Lakes Bloater—LEUCICHTHYS HOYI (Gill)

Hosts examined 47; infected 47. Parasites: *Proteocephalus laruei*—32, *Diphyllobothrium* sp.—26, *Diplostomulum* sp.—24, *Echinorhynchus salmonis*—18, *Triaenophorus crassus*—17, *Proteocephalus exiguus*—13, *Discocotyle salmonis*—5, *Cystidicola stigmatura*—4, *Echinorhynchus leidyi*—4, *Salmincola wisconsinensis*—1.

Twenty-eight of these bloaters came from deep gill nets in South Bay. Of these 27 had *P. laruei* and 10 *T. crassus* cysts, 18 *Diphyllobothrium* sp. cysts. *C. stigmatura*, *E. leidyi* and *S. wisconsinensis* were not recovered from any of the South Bay hosts.

Eleven bloaters from North Channel carried a total of 8 parasite species. Ten hosts yielded *P. exiguus*, 4 *P. laruei*, 7 *T. crassus*, 9 *Diplostomulum*, 7 *E. salmonis* and 5 *Diphyllobothrium* sp.

Seven other hosts were taken from gill nets at a depth of 60 fathoms in Lake Huron, W. of South Baymouth. These fish had the following parasites: 1 *Diplostomum* sp., 3 *Diphyllobothrium* sp., 4 *E. salmonis*, 4 *E. leidyi*, 1 *laruei* and the host with *S. wisconsinensis*. The last is a new host record.

Great Lakes Whitefish—COREGONUS C. CLUPEAFORMIS (Mitchill)

Hosts examined 99; infected 99. Parasites: *Diplostomulum* sp.—70, *Echinorhynchus salmonis*—68, *Proteocephalus exiguus*—64, *Cyathocephalus americanus*—40, *Triaenophorus crassus*—18, *Lymphocystis* sp.—15, *Cystidicola stigmatura*—13, *Spinitectus gracilis*—8, *Achtheres corpulentus*—2, *Proteocephalus laruei*—2 *Diphyllobothrium* sp.—1, *Philometra* sp.—1.

The following parasites were taken only from a few individuals of the 61 South Bay whitefish: *A. corpulentis*, *Philometra* sp. and *P. laruei*. Sixteen of the 24 hosts from Mindemoya Lake carried *T. crassus* cysts. Two from South Bay have the other *T. crassus* that was recorded. All of the *Lymphocystis* tumor cells were found about the hearts of the Mindemoya Lake fish. The *S. gracilis* cysts were in whitefish from Mindemoya Lake. No *C. americanus*, *C. stigmatura* or *E. salmonis* were recovered from hosts from this lake. All of 10 whitefish from the North Channel carried *E. salmonis* and 5 had *C. americanus*. Single hosts had *C. stigmatura* and *Diplostomulum* sp. A single host from Whitefish Lake on Mantoulin Island yielded only intestinal cestodes, *P. exiguus*.

Common Menominee Whitefish—PROSOPIUM CYLINDRACAEUM QUADRILATERALE (Richardson)

Hosts examined 22; infected 22. Parasites: *Diplostomulum* sp.—21, *Salmincola* sp.—8, *Crepidostomum farionis*—6, *Echinorhynchus salmonis*—5, *Proteocephalus exiguus*—4, *Neoechinorhynchus tumidus*—2, *Achtheres coregoni*—1, *Cystidicola stigmatura*—1, *Discocotyle salmonis*—1, *Philometra* sp.—1.

All of the hosts except one were taken from Lake Huron, near South Bay. The single fish from North Channel yielded three species of parasites: *A. coregoni, Diplostomulum*

sp. and *E. salmonis*. *N. tumidus* was described by Van Cleave and Bangham (1949) for lake herring of Trout Lake, Wisconsin and Waskesin Lake, Saskatchewan and whitefish from the latter lake. The two Menominee whitefish represent a new host for *N. tumidus*.

Rainbow Trout—SALMO GAIRDNERII IRIDEUS Gibbons

Hosts examined 15; infected 8. Parasites: *Metabronema salvelini*—6, *Echinorhynchus salmonis*—5, *Proteocephalus* sp.—3, *Abothrium crassum*—2, *Echinorhynchus leidyi*—2, *Diphyllobothrium* sp.—2, *Diplostomulum* sp.—1.

Only two of 9 hosts from Blue Jay Creek carried parasites but all of the listed forms except *Diplostomulum* sp. were taken. All of the four Manitou River rainbow trout were infected as were the two hosts from South Bay.

Common Brooktrout—SALVELINUS F. FONTINALIS (Mitchill)

Hosts examined 13; infected 10. Parasites: *Metabronema salvelini*—9, *Diplostomulum* sp.—2, *Posthodiplostomum minimum*—1, **Proteocephalus* sp.—1.

All of the six trout from the Manitou River carried light infections. The first three forms listed above were taken from certain of these hosts. Four of six from Blue Jay Creek carried *M. salvelini* and one had 15 immature *Proteocephalus* sp. One fingerling trout from Sandfield Hatchery had no parasites.

Common Lake Trout—CRISTIVOMER N. NAMAYCUSH (Walbaum)

Hosts examined 18; infected 18. Parasites: *Eubothrium salvelini*—18, *Echinorhynchus salmonis*—15, *Diplostomulum* sp.—7, *Echinorhynchus leidyi*—3.

Thirteen of the hosts were taken in South Bay and they were examined when they were brought in by line fishermen for checking by creel census workers. The infections with *E. salvelini* and *E. salmonis* were quite heavy in all of these hosts. Three lake trout from Lake Manitou had only *E. salvelini* in moderate numbers. Two hosts from Lake Huron near South Baymouth carried *E. salvelini*, *Diplostomulum* sp. and *E. salmonis*. The *E. salmonis* were very heavy in the posterior intestinal tracts of both hosts. In 22 lake trout from Algonquin Park lakes Bangham and Venard (1946) report five species of parasites. Twenty carried *E. salvelini* but all other parasite forms were different from those in Lake Huron hosts. In 1951 the writer reports on the parasites of 184 lake trout from Jackson Hole, Wyoming. Of these 175 were parasitized with a total of 11 species of parasites. Two hosts carried *E. salvelini* but all other parasite species differ from those taken in Lake Huron hosts.

Common White Sucker—CATOSTOMUS C. COMMERSONNII (Lacépède)

Hosts examined 152; infected 152. Parasites: *Diplostomum flexicaudum*—124, *Pomphorhynchus bulbocolli*—91, *Glaridacris catostomi*—52, *Neoechinorhynchus crassus*—52, *Neascus* sp.—22, *Actinobdella triannulata*—10, *Ergasilus caeruleus*—10, *Neoechinorhynchus strigosus*—10, *Myxosporidia*—7, *Octospinifer macilentus*—6, *Echinorhynchus salmonis*—4, *Ligula intestinalis*—4, *Octomacrum lanceatum*—4, *Triganodistomum attenuatum*—4, *Hepaticola bakeri*—2, *Glochidia*—1, *Plagioporus sinitsini*—1, *Echinorhynchus leidyi*—1.

Common suckers were examined from South Bay, Lake Manitou, Mindemoya Lake, Providence Bay, Windfall Lake, Big Lake and Bass Lake, near Espanola. Sixteen of the 17 parasites listed were taken from 1 to 66 of the 73 South Bay suckers. The most frequently encountered forms were found in about the same proportion in hosts from different lakes except that no *Neascus* sp. cysts were taken from South Bay hosts. Of the fish infected with eye flukes, *D. flexicaudum*, 49 hosts had less than 10 parasites, 66 had from 10 to 49 and 9 hosts carried over 50 eye flukes. *P. bulbocolli* was found in small numbers in 8 suckers, 46 had from 10 to 50 and 37 suckers had over 50 per host. Infections with other forms were light and quite scattered. *N. strigosus* was described by Van Cleave (1949) for catostomid fishes. This is the first record for a Great Lakes host.

Eastern Sturgeon Sucker, Northern Sucker—CATOSTOMUS C.
CATOSTOMUS (Forster)

Hosts examined 39; infected 39. Parasites: *Diplostomum flexicaudum*—35, *Ergasilus caeruleus*—16 *Echinorhynchus salmonis*—15, *Neoechinorhynchus crassus*—15, *Cestodaria*—11, *Neoechinorhynchus strigosus*—7, *Triganodistomum simeri*—6, *Myxosporidia*—2,

Actinobdella triannulata—1, *Echinorhynchus leidyi*—1, *Leptorhynchoides thecatus*—1, **Posthodiplostomum minimum*—1, **Triaenophorus* sp.—1.

All of the listed forms were found in some of the 28 hosts from South Bay. At least one of 11 northern suckers from Lake Huron carried individuals from the first six parasites listed above. None of the last 7 forms were taken from hosts in the open lake. *N. strigosus* and *T. simeri* are here reported as new hosts for northern suckers.

Carp—CYPRINUS CARPIO Linnaeus

Hosts examined 3; infected 3. Parasites: **Diplostomulum* sp.—2, *Dactylogyrus extensus*—1, *Pomphorhynchus bulbocolli*—1, **Spinitectus gracilis*—1.

Only three carp were examined and all came from South Bay nets.

Northern Creek Chub—SEMOTILUS A. ATROMACULATUS (Mitchill)

Hosts examined 34; infected 34. Parasites: **Posthodiplostomum minimum*—26, **Diplostomulum* sp.—23, *Allocreadium lobatum*—13, Gyrodactyloidea—10, **Neascus* sp.—5, **Myxosporidia*—2, *Rhabdochona cascadilla*—1.

All of the parasites listed were taken from some of the chubs from the Lake Manitou River at Sandfield. All of the parasites from 18 hosts in White Lake, Manitou River, were encysted.

Lake Northern Chub—COUESIS P. PLUMBEUS (Agassiz)

Hosts examined 2; infected 2. Parasites: **Diplostomulum* sp.—1, *Echinorhynchus salmonis*—1, **Posthodiplostomum minimum*—1, *Rhabdochona* sp.—1.

These chubs came from Lake Huron.

Hornyhead Chub—NOCOMIS BIGUTTATUS (Kirtland)

Hosts examined 4; infected 4. Parasites: **Diplostomulum* sp.—3, **Posthodiplostomum minimum*—3, *Allocreadium lobatum*—1, *Plagioporus sinitsini*—1.

These hosts were taken from the Manitou River.

Great Lakes Longnose Dace—RHINICHTHYS C. CATARACTAE (Valenciennes)

Hosts examined 5; infected 5. Parasites: **Posthodiplostomum minimum*—5.

These dace came from Pleasant Creek near South Bay.

Northern Redbelly Dace—CHROSOMUS EOS Cope

Hosts examined 17; infected 9. Parasites: **Diplostomulum* sp.—4, **Posthodiplostomum minimum*—3, Gyrodactyloidea—2, **Tetracotyle* sp.—1.

These individuals were collected from Rogers and McKimm creeks near South Bay. Two of 10 from Rogers Creek carried only *Diplostomum* sp.

Golden Shiner—NOTEMIGONUS CRYSOLEUCAS AURATUS (Rafinesque)

Hosts examined 4; infected 4. Parasites: **Diplostomulum* sp.—4, ***Contracaecum brachyurum*—1, Gyrodactyloidea—1.

These hosts came from Lily Lake on Manitoulin Island.

Lake Emerald Shiner—NOTROPIS A. ATHERINOIDES Rafinesque

Hosts examined 5; infected 5. Parasites: **Posthodiplostomum minimum*—5, **Myxosporidia*—1, Gyrodactyloidea—1.

Three hosts came from Providence Bay and two from South Bay.

Northern Common Shiner—NOTROPIS CORNUTUS FRONTALIS (Agassiz)

Hosts examined 6; infected 6. Parasites: Gyrodactyloidea—4, **Posthodiplostomum minimum*—4, *Rhabdochona cascadilla*—3, *Allocreadium lobatum*—1, *Lebouria cooperi*—1, *Neascus* sp.—1.

The two specimens from Pleasant Creek both carried gill flukes and one had *L. cooperi*. The latter fluke was first described from minnows of Lake Erie (Hunter and Bangham, 1932).

Great Lakes Spottail Shiner—NOTROPIS H. HUDSONIUS (Clinton)

Hosts examined 100; infected 100. Parasites: *Posthodiplostomum minimum*—80, *Diplostomulum* sp.—60, Gyrodactyloidea—56, Neoechinorhynchus rutili—23, Rhabdochona cascadilla—19, *Neascus* sp.—15, *Pomphorhynchus bulbocolli*—11, **Proteocephalus sp.—10, Allocreadium lobatum—9, *Triganodistomum* sp.—5, Lebouria cooperi—4, *Ligula intestinalis*—3, Bucephalus sp.—1, Echinorhynchus salmonis—1, Leptorhynchoides thecatus—1, Spinitectus gracilis—1, *Tetracotyle* sp.—1.

All but nine hosts came from South Bay. The single spottail shiner from the Manitou yielded cysts of *P. minimum* and *Neascus* sp. Eight Providence Bay hosts had all been infected with *P. minimum* and single individuals with eye flukes, gill flukes, *L. cooperi* and *R. cascadilla.* Bangham and Hunter (1939) report on the parasites of 94 spottail shiners from Lake Erie. Sixty-three of these were infected with a total of eleven parasite species. Six were the same as found in the Lake Huron hosts.

Blackchin Shiner—NOTROPIS HETERODON (Cope)

Host examined 1; infected 1. Parasites: *Diplostomulum* sp.—1, *Posthodiplostomum minimum*—1.

The single host was taken in South Bay.

Northern Mimic Shiner—NOTROPIS V. VOLUCELLUS (Cope)

Hosts examined 11; infected 11. Parasites: *Posthodiplostomum minimum*—10, *Diplostomulum* sp.—7, *Centrovarium lobotes*—1.

Ten hosts were from Mindemoya Lake and one from South Bay.

Northern Blacknose Shiner—NOTROPIS H. HETEROLEPIS
Eigenmann and Eigenmann

Hosts examined 25; infected 25. Parasites: *Posthodiplostomum minimum*—13, Gyrodactyloides—10, *Diplostomulum* sp.—8, **Proteocephalus sp.—5, *Spiroxys* sp.—2, *Neascus* sp.—1.

All of the parasites listed were recovered from the 19 Lily Lake hosts except for six fish from South Bay which carried only *P. minimum.*

Northern Fathead Minnow—PIMEPHALES P. PROMELAS Rafinesque

Host examined 1; infected 1. Parasites: *Neascus* sp.—1.

This host was taken in South Bay.

Bluntnose Minnow—HYBORHYNCHUS NOTATUS (Rafinesque)

Hosts examined; 17; infected 17. Parasites: *Posthodiplostomum minimum*—14, *Diplostomulum* sp.—10, *Centrovarium lobotes*—6, *Neascus* sp.—2, Gyrodactyloidea—2, Myxosporidia—1, *Rhabdochona cascadilla*—1.

Thirteen of these minnows were from Mindemoya Lake, two from Lily Lake and two from South Bay.

Northern Channel Catfish—ICTALURUS L. LACUSTRIS (Walbaum)

Hosts examined 3; infected 3. Parasites: Alloglossidium corti—3, Corallobothrium giganteum—3, Crepidostomum ictaluri—3, Gyrodactyloidea—3, Azygia angusticauda—1, **Bothriocephalus sp.—1, *Diplostomulum* sp.—1, Microphallus opacus—1.

All of the catfish came from South Bay nets.

Northern Brown Bullhead—AMEIURUS N. NEBULOSUS (LeSueur)

Hosts examined 31; infected 31. Parasites: SOUTH BAY Hosts examined 14; infected 14. Parasites: *Diplostomulum* sp.—12, Corallobothrium fimbriatum—10, Crepidostomum ictaluri—7, Acetodextra amiuri—6, Dichelyne robusta—4, Gyrodactyloidea—3, Spinitectus gracilis—2, Azygia angusticauda—1, Centrovarium lobotes—1, Microphallus opacus—1,*Pomphorhynchus bulbocolli*—1. Lake Huron, THOMAS BAY, Host examined 1; infected 1. Parasites: Acetodextra amiuri—1, Ergasilus versicolor—1. BASS LAKE, near Espanola, Hosts examined 16; infected 16. Parasites: *Proteocephalus ambloplitis*—13, Gyrodactyloidea—11, Alloglossidium geminus—11, Corallobothrium fimbriatum—9, Phyllodistomum staffordi—9, *Clinostomum marginatum*—5, Crepidostomum cornutum—5,

**Proteocephalus pearsei*—2, *Azygia angusticauda*—1, *Leptorhynchoides thecatus*—1, *L. thecatus*—1.

Western Mudminnow—UMBRA LIMI (Kirtland)

Hosts examined 4; infected 4. Parasites: *Bunoderina eucaliae*—1, *Creptotrema funduli*—1, *Diplostomulum* sp.—1, *Neascus* sp.—1, *Neoechinorhynchus rutili*—1, *Pomphorhynchus bulbocolli*—1, *Tetracotyle* sp.—1.

All of these fish came from a small stream entering South Bay.

Northern Pike—ESOX LUCIUS Linnaeus

Hosts examined 66; infected 66. Parasites: *Proteocephalus pinguis*—60, Gyrodactyloidea—37, *Contracaecum brachyurum*—35, *Triaenophorus crassus*—32, *Diplostomulum* sp.—26, *Leptorhynchus thecatus*—16, *Neoechinorhynchus cylindratus*—15, *Echinorhynchus salmonis*—14, *Azygia longa*—2, *Neoechinorhynchus rutili*—2, *Pomphorhynchus bulbocolli*—1.

Northern pike were taken from five locations: 26 from South Bay, 29 from Thomas Bay, 7 from Sheguandah Bay, 3 from Long Lake, and a single host from Bass Lake on Manitoulin Island. All of the listed parasites except *A. longa* were found in South Bay hosts. Nine of the listed parasites were secured from the Thomas Bay fish. The Long Lake and Bass Lake hosts yielded but three different parasite species. The northern pike is the definitive host of *T. crassus* which was taken from fish of all locations except the three from Long Lake.

Great Lakes Muskellunge—ESOX M. MASQUINONGY Mitchill

Host examined 1; infected 1. Parasites: *Contracaecum brachyurum*—1, *Diplostomulum* sp.—1, Gyrodactyloidea—1, *Proteocephalus pinguis*—1.

This host came from Bass Lake on Manitoulin Island.

Trout Perch—PERCOPSIS OMISCOMAYCUS (Walbaum)

Hosts examined 19; infected 19. Parasites: *Diplostomulum* sp.—15, Gyrodactyloidea—14, *Crepidostomum isostomum*—13, *Ergasilus caeruleus*—7, *Tetracotyle* sp.—7, *Echinorhynchus salmonis*—5, *Bothriocephalus formosus*—3, *Neascus* sp.—2, *Pomphorhynchus bulbocolli*—2, *Posthodiplostomum minimum*—2, *Agemonema* sp.—1, *Argulus* sp.—1, *Contracaecum brachyurum*—1, *Neoechinorhynchus* sp.—1, *Spinitectus gracilis*—1.

All of the trout perch came from South Bay.

White Bass—LEPIBEMA CHRYSOPS (Rafinesque)

Hosts examined 3; infected 3. Parasites: *Allacanthochasmus artus*—3, *A. varius*—3, *Diplostomulum* sp.—3, *Bucephalus* sp.—2, *Camallanus oxycephalus*—1, Gyrodactyloidea—1, *Leptorhynchoides thecatus*—1, *Proteocephalus ambloplitis*—1, **P. pearsei*—1, *Spinitectus carolini*—1.

All three hosts came from South Bay. White bass are rarely taken in this area. The parasites are similar to Lake Erie white bass (Bangham and Hunter, 1939).

Yellow Perch—PERCA FLAVESCENS (Mitchill)

Hosts examined 201; infected 201. Parasites: *Diplostomulum* sp.—137, *Dichelyne cotylophora*—110, Gyrodactyloidea—99, *Crepidostomum cooperi*—85, *Proteocephalus pearsei*—67, *Bunodera sacculata*—44, *Neascus* sp.—42, **Bothriocephalus* sp.—29, *Leptorhynchoides thecatus*—21, *Clinostomum marginatum*—20, *Ergasilus caeruleus*—15, *Proteocephalus ambloplitis*—14, **Rhabdochona* sp.—12, *Glochidia*—11, *Neoechinorhynchus rutili*—11, *Spinitectus gracilis*—8, *Echinorhynchus salmonis*—7, *Posthodiplostomum minimum*—7, *Illinobdella moorei*—6, *Neoechinorhynchus cylindratus*—6, *Azygia angusticauda*—4, *Leptorhynchus thecatus*—4, *Bucephalus elegans*—3, *Philometra cylindracea*—2, *Pomphorhynchus bulbocolli*—2, *P. bulbocolli*—1, *Tetracotyle* sp.—2, *Spiroxys* sp.—1. *Illinobdella alba*—1.

Certain of the 64 yellow perch from South Bay were the only hosts to the following parasites: *E. caeruleus*, Glochidia and *I. moorei*. The South Bay hosts did not have any

fish infected with *B. elegans*, *C. marginatum*, adult *L. thecatus* or *A. angusticauda*. The single host from North Channel had: *C. cooperi*, *L. thecatus*, *Diplostomulum* sp. and *E. salmonis*. The parasites from seven Manitoulin Island lakes had a scattering of different parasites. Big Lake perch had the greatest variety with 21 hosts carrying a total of 17 different species. There were 12 species found for 39 Mindemoya Lake hosts. The degree of infection was usually from light to n oderate in most hosts.

In 1946 the writer reported on the parasites of 269 yellow perch from northern Wisconsin and 261 were infected with the same total number of parasite species as found for the present hosts. Seventeen species were the same in yellow perch of the two areas.

Eastern Sauger—STIZOSTEDION C. CANADENSE (Smith)

Host examined 1; infected 1. Parasites: *Bothriocephalus cuspidatus*—1, *Centrovarium lobotes*—1, *Diplostomulum* sp.—1, *Echinorhynchus salmonis*—1, *Neoechinorhynchus cylindratus*—1.

This sauger was taken in South Bay.

Yellow Pike Perch, Pickerel—STIZOSTEDION V. VITREUM (Mitchill)

Hosts examined 41; infected 41. Parasites: *Diplostomulum* sp.—28, *Bothriocephalus cuspidatus*—21, Gyrodactyloidea—20, *Neoechinorhynchus cylindratus*—15, *Leptorhynchoides thecatus*—11, *Ergasilus caeruleus*—10, *Proteocephalus stizostethi*—10, *Neascus* sp.—6, *Bucephalopsis pusilla*—4, *Dichelyne cotylophora*—4, *Glochidia*—3, *Triaenophorus stizostedionis*—2, *Contracaecum brachyurum*—1, *Spinitectus* sp.—1.

All parasites reported in the data were recovered from individuals of the 20 Mindemoya Lake fish. Two hosts from Windfall Lake had 16 individuals with *B. pusilla*, *Diplostomulum* sp. and *L. thecatus*. Nine of 16 pike perch from Whitefish Lake had *L. thecatus*, 8 had eye flukes, while three hosts yielded immature *P. stizostethi*. Two Sandfield Hatchery fingerlings bore only eye flukes. The single host from South Bay had *B. cuspidatus*, *B. pusilla*, gill flukes and *E. caeruleus*.

Northern Log Perch—PERCINA CAPRODES SEMIFASCIATA (DeKay)

Host examined 1; infected 1. Parasites: Gyrodactyloidea—1, *Pomphorhynchus bulbocolli*—1.

This log perch was taken from South Bay.

Central JOHNNY DARTER—BOLEOSOMA N. NIGRUM (Rafinesque)

Hosts examined 39; infected 39. Parasites: *Tetracotyle* sp.—21, *Bothriocephalus formosus*—20, *Crepidostomum isostomum*—13, *Neascus* sp.—7, Gyrodactyloidea—4, *Posthodiplostomum minimum*—4, *Spiroxys* sp.—2, *Diplostomulum* sp.—2, *Dichelyne* sp.—1, *Lebouria cooperi*—1, *Leptorhynchoides thecatus*—1, *Illinobdella* sp.—1, *Neoechinorhynchus cylindratus*—1, *Rhabdochona cascadilla*—1.

The Johnny darters were taken from five locations. There was little variation in the parasites of the darters from different lakes. There were nine parasite species in the 11 Mindemoya Lake hosts.

Iowa Darter—POECILICHTHYS EXILIS (Girard)

Hosts examined 5; infected 5. Parasites: *Azygia angusticauda*—2, *Posthodiplostomum minimum*—2, *Bothriocephalus formosus*—1, *Contracaecum brachyurum*—1, *Hymenolepis* sp.—1, *Illinobdella* sp.—1, *Rhabdochona cascadilla*—1, *Tetracotyle* sp.—1.

Two of the Iowa darters came from Lily Lake and three from South Bay. The parasites in the hosts from the two areas were all different.

Northern Smallmouth Bass—MICROPTERUS D. DOLOMIEU Lacépède

Host examined 221; infected 220. Parasites: *Leptorhynchoides thecatus*—180, Gyrodactyloidea—161, *Neoechinorhynchus cylindratus*—139, *Proteocephalus ambloplitis*—121, *Spinitectus carolini*—112, *Crepidostomum cornutum*—94, *Cryptogonimus chyli*—94,

Posthodiplostomum minimum—76, *Achtheres micropteri*—60, *Diplostomulum* sp.—60, *Proteocephalus amploplitis*—36, *Dichelyne cotylophora*—29, *Clinostomum marginatum*—23, *Contracaecum brachyurum*—20, *Echinorhynchus salmonis*—18, *Microphallus opacus*—17, *Azygia angusticauda*—7, *Leptorhynchoides thecatus*—3, *Pomphorhynchus bulbocolli*—3, *Ergasilus caeruleus*—2, *Neoechinorhynchus rutili*—2, *Rhipidocotyle papillosum*—1, *Camallanus oxycephalus*—1, *Crepidostomum cooperi*—1, *Illinobdella* sp.—1, *Myxosporidia*—1, *Neascus* sp.—1, *Spinitectus gracilis*—1.

Most of these fish were brought in to the laboratory by line fishermen for creel census records. Gills and viscera were taken for parasite examination but the eyes were not examined for all hosts so the records for *Diplostomulum* sp. are not complete. Smallmouth bass were examined from four Lake Huron Bays on Manitoulin Island and from the following lakes: Windfall, Mindemoya, Manitou, Big and Whitefish. Inland Lake on Fitzwilliam Island where 20 bass were recovered with a total of 15 parasite species had *L. thecatus* as the most numerous form taken. A single host from Bass Lake, near Espanola had five parasite species but no Acanthocephala. There was quite a variation in different areas in the distribution of *C. cornutum*, *C. chyli*, *L. thecatus* and *N. cylindratus*. Seven of 8 fingerling bass from the Sandfield Hatchery had 6 with eye flukes and one host with *P. minimum* cysts. The 70 hosts from Big and Thomas bays of Lake Huron yielded a total of 22 parasite species, with gill flukes and *N. cylindratus* being the forms most frequently encountered. There were 21 different species listed for the South Bay bass with *L. thecatus* in 25 hosts, *P. ambloplitis* cysts in 24 and *N. cylindratus* from 23 fish.

Large Mouth Bass—HURO SALMOIDES (Lacépède)

Hosts examined 5; infected 5. Parasites: *Caecincola parvulus*—5, Gyrodactyloidea—5, *Neoechinorhynchus cylindratus*—5, *Crepidostomum cornutum*—3, *Azygia angusticauda*—2, *Contracaecum brachyurum*—2, *Diplostomulum* sp.—2, *Leptorhynchoides thecatus*—2, *Dichelyne cotylophora*—1, *Echinorhynchus salmonis*—1, *Microphallus opacus*—1, *Proteocephalus ambloplitis*—1, *Spinitectus carolini*—1.

Four of the largemouth bass came from Thomas Bay and the other from South Bay.

Pumpkinseed, Common Sunfish—LEPOMIS GIBBOSUS (Linnaeus)

Hosts examined 55; infected 55. Parasites: *Posthodiplostomum minimum*—52, *Neascus* sp.—49, Gyrodactyloidea—41, *Proteocephalus ambloplitis*—35, *Clinostomum marginatum*—15, *Diplostomum* sp.—14, *Crepidostomum cornutum*—8, *Leptorhynchoides thecatus*—6, *Neoechinorhynchus cylindratus*—2, *Agamonema* sp.—1, *Azygia angusticauda*—1, *Bothriocephalus claviceps*—1, *Crepidostomum cooperi*—1, *Echinorhynchus salmonis*—1, *Ergasilus caeruleus*—1, **Proteocephalus pearsei*—1, *Protometra macrostoma*—1, *Spinitectus carolini*—1.

Ten species of parasites were recovered from 21 Lily Lake hosts. Bass Lake, near Espanola yielded 7 of the parasite species from Lily Lake and 8 other forms, from 32 common sunfish. But two species were found in two hosts from Rogers Creek, near South Bay. These were *P. minimum* and *P. pearsei*.

Northern Rockbass—AMBLOPLITES R. RUPESTRIS (Rafinesque)

Hosts examined 116; infected 116. Parasites: *Diplostomulum* sp.—100, *Posthodiplostomum minimum*—100, *Spinitectus carolini*—94, Gyrodactyloidea—90, *Cryptogonimus chyli*—74, *Crepidostomum cornutum*—68, *Neoechinorhynchus cylindratus*—47, *Leptorhynchoides thecatus*—33, *Proteocephalus ambloplitis*—30, *Neascus* sp.—12, *Clinostomum marginatum*—10, *Azygia angusticauda*—4, *Achtreres ambloplitis*—4, *Ergasilus caeruleus*—3, *Illinobdella moorei*—3, *Pomphorhynchus bulbocolli*—3, *Microphallus opacus*—2, *Bothriocephalus claviceps*—1, *Camallanus oxycephalus*—1, *Contracaecum brachyurum*—1, *Crepidostomum cooperi*—1, *Dichelyne cotylophora*—1, *Echinorhynchus salmonis*—1, **Proteocephalus pearsei*—1, *Protometra macrostoma*—1.

Rock bass were taken from Mindemoya, Manitou, Windfall, Big, Long lakes and from South Bay. The 48 South Bay hosts were infected with a total of 21 different parasite species. Rock bass from Windfall and Big lakes each had the same six parasite species for 10 hosts from each lake. In addition two Big Lake hosts had *C. marginatum* cysts. The 18 rock bass from Mindemoya had light to moderate infections with 13 parasite species.

White Crappie—POMOXIS ANNULARIS Rafinesque

Host examined 1; infected 1. Parasites: *Camallanus oxycephalus*—1, *Proteocephalus pearsei*—1.

This white crappie was from South Bay.

Black Crappie—POMOXIS NIGRO-MACULATUS (LeSueur)

Hosts examined 2; infected 2. Parasites: *Camallanus oxycephalus*—1, *Diplostomulum* —1, *Gyrodactyloidea*—1, *Neoechinorhynchus cylindratus*—1, **Proteocephalus pearsei*—1, *Spiniectus gracilis*—1.

These two hosts were from South Bay and were the only black crappies taken in the experimental nets during the season.

Deep Water Sculpin—TRIGLOPSIS THOMPSONII Girard

Host examined 1; infected 1. Parasites: *Echinorhynchus salmonis*—1.

This host came from gill nets southwest of South Bay at a depth of 60 fathoms.

Great Lakes Muddler—COTTUS BIARDII KUMLIENI (Hoy)

Hosts examined 8; infected 7. Parasites: *Tetracotyle* sp.— 6, *Diplostomum* sp.—3.

These muddlers came from three sources but showed little variation in their parasites.

Brookstickleback—EUCALIA INCONSTANS (Kirtland)

Hosts examined 34; infected 33. Parasites: *Bunoderina eucaliae*—25, *Neoechinorhynchus rutili*—15, Gyrodactyloidea—8, *Neascus* sp.—5, *Diplostomulum* sp.—1, *Posthodiplostomum minimum*—1.

All of these fish except six from White Lake were taken from a small stream flowing into South Bay. In the White Lake sticklebacks there were no Acanthocephala but these hosts bore the *Neascus* sp.

Ninespine Stickleback—P. PUNGITIUS (Linnaeus)

Host examined 1; infected 1. Parasites: *Neoechinorhynchus rutili*—1.

This fish was from South Bay.

Eastern Burbot—L. LOTA MACULOSA (LeSueur)

Hosts examined 21; infected 21. Parasites: *Abothrium crassum*—20, *Echinorhynchus salmonis*—19, *Diplostomulum* sp.—17, *Haplonema hamulatum*—8, *Bothriocephalus* sp. —3, *Echinorhynchus leidyi*—3, *Neoechinorhynchus cylindratus*—2, *N. rutili*—1, *Pomphorhynchus bulbocolli*—1, **Proteocephalus pearsei*—1, *Spinitectus gracilis*—1.

All but two hosts came from South Bay. The single burbot from Mindemoya Lake carried a heavy infection of *A. crassum* and a few *S. gracilis*. The specimen from the North Channel of Lake Huron had many *E. salmonis* and small numbers of eye flukes and *A. crassum*.

SUMMARY

This survey of fish parasites was conducted during the summer of 1951 at the South Bay Fisheries Laboratory, Division of Research, Ontario Department of Lands and Forests. A total of 1,667 fish belonging to 53 different species were examined with 98.5 per cent being infected. The majority of hosts came from South Bay of Lake Huron with other bays and the open lake and lakes on Manitoulin Island being represented. *Diplostomulum* spp. were secured from the eyes of 939 hosts belonging to 44 different fish species. *Posthodiplostomum minimum* cysts were recovered from 411 hosts belonging to 22 different species. Fewer *Neascus* sp. cysts were encountered than in previous surveys. *Echinorhynchus salmonis* were recovered from 242 hosts belonging to 23 species of fish. Other species of Acanthocephala were often taken. *Triaenophorus crassus* cysts were most frequently recovered from the flesh of lake herring from South Bay. Certain Great Lakes bloaters and

Mindemoya Lake whitefish also carried *T. crassus* cysts. Adult *T. crassus* were recovered only from the intestinal tracts of northern pike. *Diphyllobothrium* sp. cysts were found in 54 of 79 lake herring and from 26 of 47 Great Lakes bloaters. A few new hosts for parasites are listed for these Lake Huron fish species.

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Trematodes Parasitic in the Salientia in the Vicinity of Ann Arbor, Michigan*

Haig H. Najarian
University of Michigan, Ann Arbor

With the exception of the studies by Krull (1931), Krull and Price (1932), and Hunt (1950), this paper constitutes the only published report on adult trematodes parasitic in the Salientia in the vicinity of Ann Arbor, Michigan. Excluding the species of these cycles, the trematodes reported here constitute new distributional records, and in three cases, new host records.

Materials and methods.—The 102 hosts used in this study were collected during April through September, 1951, from four stations in the vicinity of Ann Arbor, *viz.*, ponds along Zeeb Road, Whitmore Lake, Flemming Creek, and the Huron River. Most of the amphibians were killed within 48 hours after capture. The worms were fixed with hot A.F.A. Borax carmine, Mayer's paracarmine, and Delafield's hematoxylin were used as stains.

Brachycoelium salamandre (Froelich) Dujardin, 1845. HOSTS: *Acris gryllus, Rana sylvatica.* POSITION: Small intestine.—There is considerable difference of opinion in regard to the number of valid species in the genus. Those reported exhibit wide variability in regard to size, shape, and position of specific characters. Rankin (1938) made a comprehensive study of the genus and reduced the 12 reported North American species to synonymy with the type, *Brachycoelium salamandrae* (Froelich) Dujardin, 1845. On the basis of his study, and until a knowledge of the life history is obtained, this opinion seems sound.

Glypthelmins quieta (Stafford, 1900) Stafford, 1905. HOSTS: *Hyla crucifer, Rana clamitans, R. catesbeiana.* POSITION: Small intestine.—Leigh (1938), in an abstract, described the life history. Rankin (1944) gave a review of the genus with an account of *G. quieta.* Leigh (1946) reported the details of the life history. Frogs become infected upon eating cast skin harboring the metacercariae. Arboreal forms, such as *Hyla crucifer,* must become infected only during the months of the breeding season.

Cephalogonimus americanus Stafford, 1902. HOSTS: *Rana clamitans, R. pipiens.* POSITION: Small intestine.—Bouchard (1951) was in error when he reported *R. clamitans* as a new host for this species. Stafford (1902, 1905) reported it from *R. clamata,* which, according to Stejneger and Barbour (1943) is a synonym of *R. clamitans.* The life history is unknown.

Cephalogonimus vesicaudus Nickerson, 1912. HOST: *Rana clamitans.* POSITION: Small intestine.—As far as can be determined, this species has been reported only from soft-shelled turtles (Nickerson, 1912). The life cycle is unknown.

Gorgodera amplicava Looss, 1899. HOST: *Rana clamitans.* POSITION: Urinary bladder, ureter.—Krull (1935) reported the life history. The clam, *Musculium partumeium* serves as first intermediate host; the fresh-water snail, *Helisoma antrosum* as second intermediate host. Frogs become infected by eating snails harboring the metacercariae.

Gorgoderina simplex (Looss) Looss, 1902. HOSTS: *Rana clamitans, R. catesbeiana.* POSITION: Urinary bladder.—Although the life history of *G. simplex* is unknown, the cycle of a closely related species, *G. attenuata,* was reported by Rankin (1939). The clam, *Sphaerium occidentale,* serves as first intermediate host. Tadpoles ingest the cercariae which then penetrate the gut wall and encyst in the body cavities and organs. Frogs become infected by eating tadpoles harboring the metacercariae.

Megalodiscus temperatus (Stafford, 1905) Chandler, 1923. HOSTS: *Rana catesbeiana, R. clamitans, Hyla crucifer.* POSITION: Large intestine.—Krull and Price (1932) demonstrated the life cycle. The snail, *Helisoma trivolvis,* serves as first intermediate host. Amphibians become infected by devouring molted skin harboring the metacercariae.

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Haemotoloechus varioplexus Stafford, 1902. HOST: *Rana sylvatica.* POSITION: Lungs.—The life history is unknown.

Haematoloechus parviplexus (Irwin) Ingles, 1932. HOST: *Rana clamitans.* POSITION: Lungs.—Krull (1931) reported the life cycle. The snail, *Gyralus parvus,* serves as first intermediate host. Dragon flies of the genus *Sympctrum* serve as second intermediate host.

Haematoloechus breviplexus Stafford, 1902. HOST: *Rana clamitans.* POSITION: Lungs.—The life history is unknown.

Haematoloechus longiplexus Stafford, 1902. HOST: *Rana catesbeiana.* POSITION: Lungs.— Krull (1932) reported the second intermediate host of this cycle to be damsel flies of the genus *Lestes.* The snail host was not determined.

Clinostomum attenuatum (metacercariae) Cort, 1913. HOST: *Rana clamitans.* POSITION: Muscles, mesenteries, body cavity, and tongue.—Price (1937) reported the adult from the chicken. The snail host is not known.

Gorgoderid metacercariae. HOST: *Hyla crucifer, Rana sylvatica, R. clamitans.* POSITION: Urinary bladder, kidney, mesenteries on stomach.

Echinostome metacercariae. HOST: *Hyla crucifer, Rana clamitans, R. sylvatica.*— Feeding experiments with chicks (Najarian, 1952), showed these cysts to be the metacercaria of *Echinoparyphium flexum* (Linton, 1892) Dietz, 1910. Linton (1892) described the species from the black scoter. McCoy (1928) reported the cercaria from *Helisoma trivolvis* and found the cercaria to encyst in both *Physa integra* and *H. trivolvis.*

TABLE 1.—Summary of hosts and parasites

Host	Number Examined	Percent Infected	Parasite
Acris gryllus	2	100	*Brachycoelium salamandrae**
Bufo terrestris	5	....	
Hyla crucifer	5	80	*Glypthelmina quieta*
		67	gorgoderid cysts
		100	echinostome cysts
		20	*Megalodiscus temperatus*
H. versicolor	5	....	
Rana sylvatica	36	19	*Haematoloechus varioplexus*
		11	*Brachycoelium salamandrae**
		42	echinostome cysts
		18	gorgoderid cysts
R. pipiens	5	20	*Cephalogonimus americanus*
		20	Renifer cysts
R. clamitans	40	48	*Haematoloechus parviplexus*
		42	*H. breviplexus*
		10	*Gorgoderina simplex*
		15	*Gorgodera amplicava*
		7	*Glypthelmins quieta*
		30	*Cephalogonimus americanus*
		5	*C. vesicaudus**
		12	*Megalodiscus temperatus*
		4	*Clinostomum attenuatum* cysts
		14	echinostome cysts
		7	gorgoderid cysts
R. palustris	1	....	
R. catesbeiana	3	33	*Gorgoderina simplex*
		66	*Megalodiscus temperatus*
		33	*Glypthelmins quieta*
		33	*Haematoloechus longiplexus*

* New host record.

Renifer metacercariae. HOST: *Rana pipiens.* POSITION: Mesenteries.

Summary.—One hundred two amphibians, consisting of nine species of Salientia, were collected in the vicinity of Ann Arbor, Michigan and examined for flukes. Eleven species of adult trematodes and four species of metacercariae were recovered. Three new host records are reported. With three exceptions, the reported parasites constitute new distributional records. The life histories of the reported worms, when known, are given. An error in the literature is indicated.

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Neascus nolfi n. sp. (Trematoda: Strigeida) from Cyprinid Minnows with Notes on the Artificial Digest Recovery of Helminths

Glenn L. Hoffman

University of North Dakota, Grand Forks

During an examination of fish from Turtle River, Arvilla, North Dakota, a new *Neascus* (larval strigeid) was recovered from the musculature and integument of the northern creek chub, *Semotilus a. atromaculatus* (Mitchell) and the northern common shiner, *Notropis cornutus frontalis* (Agassiz). This new species is named in honor of Dr. L. O. Nolf, University of Iowa.

Neascus nolfi n. sp.

The following description is based mostly on living material except for the measurements, which were all done on metacercariae freed from their cysts, fixed in hot AFA, and stained with celestin blue B.

The outer host cyst is heavily pigmented, is nearly spherical, and ranges from 472 to 576μ in diameter. The inner thin cyst, which is probably of parasitic origin, is also nearly spherical and measures between 202 and 324μ in diameter. It cannot be separated easily from the host cyst as is the case with *Uvulifer* (*Neascus*) *ambloplitis*. However, the metacercaria itself of *N. nolfi* is more easily freed from the cyst with the use of small forceps and needle.

The metacercaria, which is clearly divided into fore and hind bodies, measures 290-382μ (340 average of 4) in length and 137-153μ (147 average of 4) in greatest width. The forebody, which is thin, flat and leaf-shaped with posterior edges forming a shallow cup like most Diplostomatidae metacercariae, averages 229μ in length by 147μ in greatest width. In living worms, the great width of the forebody is very striking even while still in the cyst. The conical, rounded hindbody measures 61-107μ in length by 52-61μ in greatest width. The oral sucker is 44μ wide x 41μ long and faces anteroventrally. No prepharynx could be seen. The pharynx measures 13 x 12μ and the esophagus is 24 to 27μ long. The intestinal crura can be seen extending into the hindbody in stained specimens but the terminations could not be ascertained; they could not be seen at all in unstained worms. The ventral sucker, which is located about mid-way in the forebody, is 17μ in diameter. The round holdfast organ is approximately 55μ in diameter.

In no instances could a reserve bladder of the excretory system be discerned; this is unusual in a *Neascus*. There is little likelihood that these are "young" forms of other *Neascus* species in which the reserve bladder system has not yet developed, because the host cyst is already pigmented. In the only black-spot *Neascus* which has been studied experimentally, the metacercaria is fully developed by the time the cyst becomes melanated (Hunter and Hamilton, 1941).

No evidence of reproductive fundament or holdfast gland could be discerned.

Neascus nolfi differs from: (1) *Uvulifer* (*Neascus*) *ambloplitis* (Hughes, 1927) in the more spherical shape and larger size of the parasite cyst, smaller size of the metacercaria, lack of reserve excretory system and intolerance of pepsin solution; (2) *Crassiphiala* (*Neascus*) *bulboglossa* (Van Haitsma, 1925) in the round shape and smaller size of the parasite cyst, smaller size of the metacercaria, lack of reserve excretory system, and in possession of a ventral sucker; (3) *N. pyriformis* Chandler (1951) in the round shape of the parasite cyst, smaller size of the metacercaria, and lack of reserve excretory system; (4) *N. ellipticus* Chandler (1951) in the round shape and smaller size of the parasite cyst, smaller size of the metacercaria, lack of reserve excretory system, and in possession of

host cyst pigmentation; (5) *N. rhinichthysi* Hunter (1933) in the absence of a discernible reserve excretory system and the smaller size of the metacercaria.

The type specimen has been deposited in the United States National Museum Collection as No. 47898.

PEPSIN DIGEST OF FISH

Because *Neascus nolfi* and gasterostome metacercariae had been digested and overlooked during routine digest of fish tissue it was decided to compare three methods of isolating trematode larvae: (1) Routine pepsin digest followed by saline washings; (2) Waring blendor maceration of tissue followed by a very short pepsin digest and saline washings; (3) Waring blendor maceration followed only by saline washings.

The pepsin solution digest method of freeing encysted nematode and trematode larvae has been used by many workers and has been particularly useful in *Trichinella spiralis* studies. Its usefulness is great but since not all larvae can tolerate pepsin solution for very long, and some cannot tolerate it at all, it must be used with caution. Hemenway (1948), Hughes (1928c), and Wallace (1935, 1939) have used trypsin to assist metacercariae in excysting, and Lyster (1940) has used the plant proteolytic enzyme, papain, for liberating *Trichinella spiralis* larvae.

A water bath shaker was used which consists of a metal basket that fits inside the bath and is powered by a geared-down Kahn shaker. The unit makes 72 excursions per minute, and the digest bottles are held to the basket by natural rubber strips from discarded automobile inner tubes. A temperature of 39°C was chosen instead of 37°C because most of the worms recovered were those which develop to maturity in birds, and it was hoped that the 2°C increase would hasten digestion.

The digest solution consisted of 0.5% pepsin in 0.25% HCl made up in 0.65% 3-salt Ringer's (Parker, 1938). One percent HCl has been used by most workers, particularly for *Trichinella* digest, but I hoped to minimize the possibility of acid damage to the worms. I had previously found pH2 and
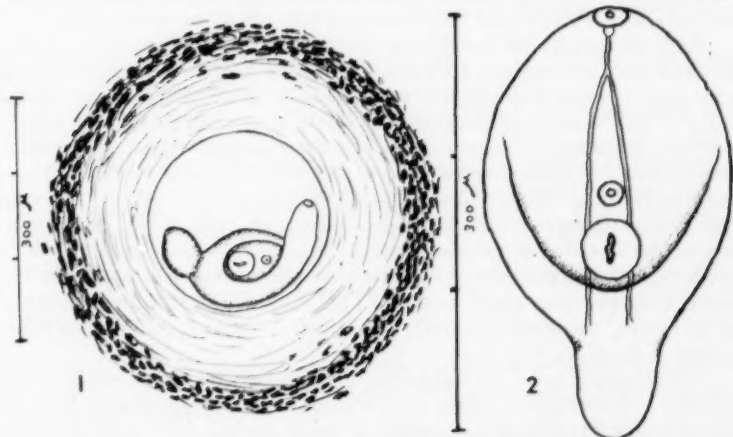
Figs. 1, 2.—1. Free hand drawing of living *Neascus nolfi* within the cyst.
2. Composite drawing of living, and fixed and stained *Neascus nolfi*.

lower to be inimical to the survival of the metacercariae of *Posthodiplostomum minimum* (Hoffman, 1950). Washings were made with 0.65% 3-salt Ringer's The digest solution was used in the approximate proportion of 20 cc of solution to 1 gram of tissue.

Routine digestion consisted of cutting the fish into small pieces and digesting until the material appeared all digested. Rapid digestion consisted of macerating the tissue for 1 minute in the Waring blendor and then digesting for 10 to 15 minutes; this was used for muscle and integument. For viscera, the Waring blendor was omitted. The parasites were allowed to settle and the solution was decanted, followed by three or four saline washings.

Neascus nolfi was first observed after the rapid digestion technique. Although metacercariae of the common black-spot *Neascus, Uvulifer ambloplitis*, were alive after this treatment, none of the new metacercariae were. The cysts remained intact, however, and the gross morphology of the larvae did not appear distorted. One to 8 minutes in the Waring blendor followed by saline washing with no pepsin digest yielded a few living metacercariae which appeared normal in all respects. It was extremely difficult to macerate the tissue just enough in the Waring blendor to free large numbers of the cysts but not to damage them; consequently, only a few could be recovered alive from each infected fish. It was impossible to determine accurately the number of larvae present or the number of fish infected except that they were far less numerous than *U. ambloplitis* in the final samples. During routine pepsin digestion of fish no *Neascus nolfi*, gasterostome metacercariae, or cestode larvae were recovered although it was known that all were present. Only a few *Posthodiplostomum minimum* metacercariae survived the routine method, although the fish were heavily infected. Nematode larvae remained alive and active. *Uvulifer ambloplitis* metacercariae survived this treatment, and many were active and appeared uninjured, but they failed to survive when transplanted into the muscle or visceral cavity of the same species of fish. When recovered from Waring blendor washings only, both *U. ambloplitis* and *N. nolfi* were alive 5 weeks after transplantation into fish of the same species.

In an attempt to free readily the intestinal nematode *Rhabdochona cascadilla*, and the metacercariae of *Posthodiplostomum minimum, Ornithodiplostomum ptychocheilus*, and other helminths present in the viscera, it was found that a 10 to 15-minute pepsin digest in a 39°C water-bath shaker was satisfactory. The intestine and stomach were slit open previous to digestion. Adult *Rhabdochona cascadilla, Phyllodistomum* spp., and *Allocreadium lobatum* were recovered intact and alive and freed of all mucus. The visceral metacercariae were alive and nearly all of them were freed from their cysts. Many other workers have used a pepsin digest technique for recovering larval helminths but, to my knowledge, there is no record of others using it to free adult helminths from the mucus and mucosa. This method proved more satisfactory for recovering intestinal helminths from mucus than the 0.7% $NaHCO_3$ method of Bangham (1951).

The following larval trematodes have been found to survive pepsin digest methods: *Amphimerus elongatus* (Wallace, 1939); *Apophallus venustus* (Cameron, 1945); *Caecincola parvulus*, 2 hrs. (Lundahl, 1941); *Clinostomum marginatum* (Hemenway, 1948; Nolf, 1952); *Diplostomulum corti* (Hoffman, 1953a); *Fibricola cratera, ibid; Metorchis conjunctus* (Cameron, 1945);

Ornithodiplostomum ptychocheilus (this paper); *Posthodiplostomum mini-mum* (Ferguson, 1940; Hoffman, 1950, 1953b; this paper); *Sellacotyle mustelae* (Wallace, 1935); *Uvulifer ambloplitis* (Nolf, 1952; this paper); An uniden-tified distome metacercariae in musculature of the brown bullhead (Hoffman, 1953a).

The following have been found not to survive pepsin digest methods: Gasterostome metacercariae, can be recovered dead after 10 min. digest (Hoff-man, 1953a); *Linstowiella szidati*, can be recovered dead (Anderson and Cable, 1950); *Neascus nolfi*, can be recovered dead (this paper); an unidenti-fied distome metacercaria in the mucosa of the creek chub can be recovered dead after 10 min. digest (Hoffman, 1953a).

KEY TO THE KNOWN LARVAL STRIGEIDS OF NORTH AMERICAN FISH*

1. Typical strigeid constriction lacking but holdfast present; no lateral pseudo-suckers or cotylae; no ventral sucker ....Cyathocotylidae 2

   Typical strigeid constriction present although sometimes reduced; if no evidence of constriction there are lateral pseudo-suckers or cotylae 3

2. In flesh of cyprinids; cyst nearly round, about 180μ; adult exp. in unfed chicks (Anderson and Cable, 1950) ....*Linstowiella szidati*

   In flesh of centrarchids; possibly adult in snakes; much like *L. szidati* above (also

   a *Prohemistomulum* in Europe; Ciurea, 1930) (Vernberg, 1952) ....
   ....*Prohemistomum chandleri*

3. Encysted forms 4

   Not encysted; two lateral pseudo-suckers; hind body usually not apparent; usually in eyes, one sp. in musculature, one sp. in brain ....
   ....*Diplostomulum* sp. and *Diplostomum* sp.1

   a. In lens of many spp. fish; adult in gulls (Hughes and Berkhout, 1929) ....
   ....*Diplostomum flexicaudum*

   b. In musculature of Siluridae; large (1 mm); adults in cormorants and herons. (Ciurea, 1930; Hugghins, 1953)........(*Diplostomulum corti*) *Hysteromorpha triloba*

   c. In vitreous humor; over 3 times as long as broad (Hughes, 1929b) ....
   ....*Diplostomulum scheuringi*

   d. In optic tecti and in cyst-like structure at posterior of optic tecti of *Eucalia in-constans* (Hoffman, 1953; to be described later) ....*Diplostomulum* sp.

   e. In vitreous humor; less than 3 times as long as broad; adult in gulls ....
   ....*Diplostomum huronense* and *Diplostomulum* spp.2

4. Two lateral cotylae (suckers); in pericardial cavity, visceral cavity, and eye muscle; cyst nearly round; in many spp. fish ....*Cotylurus* (*Tetracotyle*) sp.

   Adult demonstrated in one instance in the intestine of gulls; known as *Coty-lyrus communis* (*Tetracotyle communis* Hughes, 1928). Hughes (1928a) described 3 other sp. of *Tetracotyle* but because of the difficulty in identify-ing spp. of this genus the metacercariae are known as *Tetracotyle* sp. unless shown by experimentation to be metacercariae of known spp. Further life history is needed on this group.

   No lateral cotylae 5

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* The references in parentheses are not necessarily those of the original author.

1 *Diplostomulum* denotes larval genus where adult is unknown; perhaps is the meta-cercaria of *Diplostomum* sp.

2 If a *Diplostomulum* is not readily identified as one of the first 4 spp. it is desig-nated as *Diplostomulum* sp. Further life history work is needed to straighten out this group.

5. In cranial cavity of *Notropis cornutus frontalis* and *Pimephales p. promelas*; small oval cyst; adult in chick exp.; (Hoffman, 1954)....*Ornithodiplostomum ptychocheilus*

   In viscera, mesenteries, peritoneum 6

   In musculature and integument 7

6. Relatively short hindbody; constriction slight; relatively small (cyst 750μ); in mesenteries of Cyprinidae; adult in mergansers, squaw duck, and exp. in domestic duck and unfed chick (Hughes and Piszcek, 1928; Van Haitsma, 1930; Hoffman, 1954 ....*Ornithodiplostomum ptychocheilus*

   Relatively large hindbody; constriction pronounced; much larger (metacercaria over 1 mm); adults in herons, exp. in unfed chicks ....*Posthodiplostomum* sp.

a. In liver, kidneys and on heart of centrachids (Ferguson. 1943: Hoffman, 1950; Hughes, 1928b; Van Cleave and Mueller, 1934:249) ......*P. minimum centrarchi*

   b. In mesenteries of cyprinids (Hughes, 1928b; Hoffman, 1950) ....*P. m. minimum*

   c. In mesenteries of *Umbra limi*; forbody very large; ventral sucker in center of forebody; adult unknown (Mueller and Van Cleave, 1932:93) ....*Neascus (Posthodiplostomum?) grandis*

7. Black pigment surrounding cyst 8

   No black pigment surrounding cyst 13

8. Metacercaria nearly fills the parasite cyst 9

   Metacercaria does not fill the parasite cyst 12

9. Parasite cyst pyriform 10

   Parasite cyst oval or round 11

10. Parasite cyst about 330 x 200μ; in many fish; adult in kingfisher (Hughes, 1927) ....*Uvulifer (Neascus) ambloplitis*

    Parasite cyst smaller (about 270 x 160μ), abruptly narrowed at one end; in perch; adult not demonstrated, possibly is *Uvulifer semicircumcisus* in kingfisher. (Chandler, 1951) ....*Neascus pyriformis*

11. No ventral sucker; reserve excretory system similar to that of *N. ambloplitis* but forebody greatly cup-shaped (Hughes, 1928c) ....*Crassiphiala (Neascus) bulboglossa*

    Ventral sucker present; reserve excretory system similar to *N. ambloplitis* although simpler; in dace; adult unknown (Hunter, Wanda, 1933) ....*Neascus rhinichthysi*

    12. Smaller (parasite 200 to 330μ); reserve excretory system indistinct; in *Semotilus a. atromaculatus, Notropis cornutus frontalis*, possibly others; adult unknown (this paper) ....*Neascus nolfi*

    Quite large (parasite cyst 450μ long, metacercaria 870μ long); metacercaria with a finger-like anterior papilla; in perch; adult unknown (Chandler, 1951) ....*Neascus longicollis*

13. Oral sucker smaller than ventral sucker; parasite cyst 570μ long; metacercaria 760μ long; resembles *P. minimum* somewhat; in perch; adult unknown (Chandler, 1951) ....*Neascus ellipticus*

    Oral sucker larger than ventral sucker; parasite cyst about 1 mm long; metacercaria about 1½ mm long; in perch, pike, cyprinids IN EUROPE, adult in pelicans, Europe and U.S. (Ciurea, 1930; Dubois, 1938:158) ....*Bolbophorus confusus*

I wish to thank Dr. Asa C. Chandler, Rice Institute, Houston, Texas, for reading the manuscript and for suggestions concerning the preparation of the above key.

Summary

A new strigeid metacercaria, *Neascus nolfi*, from the creek chub, *Semotilus a. atromaculatus*, and shiner, *Notropis cornutus frontalis*, is described.

Neascus nolfi, gasterostome metacercariae, and a distome metacercaria in the stomach mucosa of the chub do not survive pepsin digest whereas *Uvulifer (Neascus) ambloplitis, Posthodiplostomum minimum, Ornithodiplostomum ptychocheilus, Diplostomulum corti, Fibricola cratera,* and an unidentified distome metacercaria in the musculature of the bullhead do survive for varying lengths of time. The adult helminths, *Phyllodistomum* sp., *Allocreadium lobatum,* and *Rhabdochona cascadilla* can be freed from mucus and mucosa by 10 to 15-minute exposure to pepsin solutions.

A key to the strigeid metacercariae of North American fish is presented.

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The Concept of Psephonecrocoenosis Applied to "Dwarf" Fossil Faunas

Paul Tasch

North Dakota Agricultural College, Fargo

ABSTRACT

Any explanation of dwarfed fossil faunas is subject to two persistent limitations: 1) small size of all individuals, 2) mixed populations. When appeal to biological processes (dwarfing by iron, salt or phosphorus) is disqualified, sedimentary or related processes are invoked (size calibration by current action; natural sieves).

The sieving theory is applicable to a grade-size analysis of a sample of an entire fossil fauna. Such an analysis of the Pennsylvanian "Dry shale" fauna is given. The fauna is termed a *psephonecrocoenosis* and consists largely of juveniles. Occurrence of dwarfed individuals in any *psephonecrocoenosis* or association of assemblages of small fossils and oolites, phosphate pebbles, and sea balls is attributed to bottom sorting. Association of such assemblages with black carbonaceous shales is attributed to natural sieve action.

The presence of organic matter in sediments on a regional scale may be indicated by both small- and large-sized pyritized faunas, as well as by widely distributed species such as *Gonioloboceras goniolobum* which experienced high seasonal mortality of the young.

LIMITING CONDITIONS

Any explanation of "dwarf," "depauperate," or "diminutive" fossil faunas is invalid unless it satisfies a set of limiting conditions. These conditions are: 1) size, 2) composition. Regarding size, most faunas of these types (e.g., Tully, Salem, Maquoketa) consist of individuals which fall predominantly into pebble (8.0 mm-4.0 mm) or granule (4.0 mm-2.0 mm) grade sizes. This holds true regardless of the composition of the fauna or its geologic age. As for composition, different species and different components (gastropods, pelecypods, ammonoids, etc.) occur together. Thus, any explanation that can account for a mixed assemblage of fossils but that does not simultaneously explain the uniformly small size of all fossils in the assemblage, must be ruled out.

The general interpretation of faunas of the above types fails to take into account both the limiting or necessary conditions, since reliance has been placed upon biological processes. Thus retardation of growth in marine invertebrates has been attributed to biological effects of salt, iron, phosphorus, etc. Such factors have been thought to be sufficient to account for the uniformly small size of some fossil faunas (Tasch, 1953, Part II). But are they? Do any known biological processes operate on diverse assemblages of marine invertebrates (limiting condition 2) so as to produce an entire fauna of predominantly pebble or granule size (limiting condition 1)?

Biological literature gives a negative answer to this question (Tasch, *idem*). All available evidence indicates that the end results of biological processes are variation and individual difference in everything; non-uniformity seems to be the rule. This holds for different marine invertebrates regardless of what aspect of their life and function we consider: ionic regulation, diet, ecological niche, locomotion, or size attained at a given growth stage. It follows from this that

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the uniformly small size of a fossil fauna is unlikely to have a biological explanation.

How then can we satisfy the limiting conditions, namely, distinctly small size that characterizes all individuals in a mixed population that includes members of several phyla and orders? The most plausible alternative, once appeal to biology is ruled out, is to invoke sedimentary processes. The end result of such processes as sieving and selective bottom sorting must be relative uniformity in size or a reasonable approximation of this ultimate condition. Among the possibilities are size calibration by wave and current action, and by natural sieves.

Size calibration by current action.—Reports of the influence of wave and current action in sorting living marine invertebrates by size are rare. If investigators were oriented to look for such evidence, however, reports might occur more frequently. Thus Myers (1943:439-457) found that in one region samples of a population of the foraminifer *Elphidium crispium* had been sorted according to size as a result of winter turbulence. The occurrence of an apparent "dwarf" race of English lobsters also has been explained by current sorting (Graham, 1949:481-483).

Size calibration by natural sieves.—Colonial organisms such as sponges and prolific algae (*Algenwald*) effectively sieve out small (fry) from large (adult) marine invertebrates (Fuchs, 1871:204-206; Mann, 1948:9-332; Kühn, 1936:255-268). Myers (*op. cit.*) found that a sample of 1 cc taken from a tide pool contained about one thousand animals living in association with coralline algae. Of these, one-half were foraminifers. The mollusks, annelids, arthropods, bryozoans, and nematodan associates were either minute species or juvenile stages of larger species.

Studies of animals living on kelp in the San Juan channel (Andrews, 1925:25-27) revealed upward of forty species and 2,605 individuals associated with nine holdfasts. Of these, the crabs, sea urchins, etc. were the young of larger species. Adults of worms, brittlestars, and amphipods were also present in large numbers. While the data given do not provide sizes of these adults, it is reasonable to conclude that they were adults of species with a low upper-size limit. Hence, they could live on or cling to the holdfasts along with juveniles of other species. In instances such as this, the holdfasts do not actually act as sieves as do sponges or an *Algenwald*. Rather, sieve-action is simulated by the space limitations on each holdfast. Fenton (personal communication, May 6, 1953) questions this for brittlestars in the San Juan channel, however, since he has observed that they are of various sizes and cling to the holdfasts with their arms. Further, he doubts that they are "sieved for size." It is quite possible that the simulated sieve-action discussed above, while applicable to most of the holdfast fauna, does not apply to forms well equipped for clinging, such as the brittlestars.

Turning to the fossil record, we find that a recent study of cephalopods in Ordovician to Cretaceous pyritic faunas indicates that the goniatites are not dwarfs but juvenile individuals which have experienced a high infantile mortality. The authors suggest that pyritic faunas have in general lived among marine meadows (*les herbiers*) (Termier and Termier, 1951:16-26).

If sediments containing "dwarfed" faunas indicate the one-time existence

of meadows, as do black carbonaceous shales, the small size of the fossils may be attributed to natural sieving action. If such evidence is lacking, however, it seems unwise to appeal to natural sieves as an explanation for the small size of an entire fossil fauna as has been done for that of the Kaibab (Chronic, 1952:95-166) and some other formations (Termier and Termier, *op. cit.*). In such situations selective sorting by current action offers a preferable explanation.

In terms of current sorting, it matters little that any given sample consists of fifty or more distinct species. These fossils may be viewed as clastic particles whose movement is governed by the same factors as those governing grains of sand or gravel. In the present paper, evidence for selective sorting by current action is given for the Pennsylvanian "Dry shale" fauna of Kansas.

Theoretical Considerations

The true nature of a "dwarf" fauna can be told only if we know whether its fossils are small adults of species normally large, full-sized adults of normally small species, or young and therefore small specimens. Only those forms can be used, therefore, whose growth stages can be readily determined or reliably inferred from morphological characters.

In studying the "Dry shale" fauna, specimens were individually measured under the microscope using a micrometer eyepiece with 100 divisions in 10 mm. Three diameters (length, width or height and thickness) were determined in addition to other measurements. The long diameter alone was used as the basis for determining grade-size distribution in the entire sample.

Certain questions may arise as to the validity of translating grade-size analysis concepts, based on sieving theory, to a sample of an entire fauna whose dimensions were determined by individual measurements. Still others may arise regarding choice of parameters. Table 1 was prepared to illustrate the grade-sizes that will be assigned if mean diameter instead of long diameter alone is used.

For cephalopods which are nearly spherical, with rare exceptions, the grade-size will be the same whether it is determined by mean diameter or by the long diameter only. For brachiopods, pelecypods, and gastropods, grade-size based on long diameter only can be identical with that based on mean diameter. This is so because there are a 4 mm and a 2 mm leeways for small pebbles and granules respectively. Or, using mean diameter, the grade-size will often be *one grade-size less* than that assigned when long diameter is used. The table of fossil size distribution (table 2), while concealing a probable error of a portion of one grade-size, will not alter the conclusion that a given fauna (8 mm-4 mm) is a pebble/granule necrocoenosis. The term "necrocoenosis" as used here denotes an assemblage of dead animals as represented by their fossilized remains. The term further denotes that the assemblage as found in the fossil record does not constitute a once-living community of animals, but is an artificial community in which mixing of species was accomplished by current action after death. The grade-size prefix "pebble/granule" indicates that size calibration within this range characterizes the given fossil assemblage. It should be noted that size calibration by current action is not a necessary or always present characteristic of every necrocoenosis.

Even though what is designated in this paper as a small pebble necrocoenosis (psephonecrocoenosis) may be more accurately described as a granule necro-

TABLE 1.—Comparison of two methods of grade-size determination for an entire fauna as represented in a given collection

Fossil Name	Fossil Specimen Number[a]	Diameter				Grade-Size By Using	
		Longest (A) (mm)	Inter-mediate (B) (mm)	Shortest (C) (mm)	Mean (D) (mm)	(D) (mm)	(A) (mm)
CEPHALOPODS:[b]	1	7.8	6.2	3.3	5.5	8-4	8-4
Imitoceras grahamense	6	6.1	5.0	3.2	4.4	8-4	8-4
	11	5.2	4.2	3.8	4.4	8-4	8-4
Gonioloboceras goniolobum	1	7.7	4.0	2.9	4.9	8-4	8-4
	6	6.3	5.4	3.4	5.0	8-4	8-4
	11	9.3	7.6	4.4	7.1	8-4	16-8
BRACHIOPODS:	1	4.3	3.9	2.5	3.5	4-2	8-4
Crurithyris planoconvexa	6	4.7	4.4	2.9	3.0	4-2	8-4
	11	6.0	5.9	2.5	4.8	8-4	8-4
PELECYPODS:	1	24.2	9.0	4.6	12.9	32-16	32-16
Nuculana bellistriata	6	9.6	5.0	3.0	5.9	8-4	16-8
	11	9.4	4.5	2.6	5.5	8-4	16-8
Anthracoeneilopsis kansana	1	6.9	4.4	2.7	4.7	8-4	8-4
	6	6.1	3.9	2.5	4.2	8-4	8-4
	11	6.5	4.2	2.7	3.3	4-2	8-4
Schizodus piedmontensis	1	6.2	5.7	3.1	5.0	8-4	8-4
	6	6.6	6.1	2.9	5.2	8-4	8-4
	11	9.0	8.0	3.5	6.8	8-4	16-8
GASTROPODS:	1	4.7	3.7	....	....	4-2[c]	8-4
Kansana discoidalia	6	7.9	6.7	....	....	8-4	8-4
	11	8.6	7.8	....	....	8-4	16-8
Euphemitella emrichi	1	5.5	3.9	....	....	4-2[c]	8-4
	6	4.2	3.3	....	....	4-2	4-2
	11	2.8	2.0	....	....	4-2	4-2

[a] Specimens were selected at random, every fifth specimen starting with number one. The figures cited are culled from a tabulation of 7,000 measurements.

[b] Only certain elements of the "Dry shale" fauna are given for illustration. For complete fauna see Tasch, op. cit., Pt. I.

[c] Grade-size determined on basis of intermediate diameter only.

coenosis in terms of mean diameter, equivalent current sorting competence is involved. It is well established that a current velocity competent to move coarse sand and pebbles is proportional to the square root of the diameter of the grains.

In making a grade-size analysis of a sample of an entire fauna, the sieving theory is applicable when elements of such fauna fall in the pebble-granule size

TABLE 2.—Grade-Size analysis of the "Dry shale" limonitic fauna regardless of species, and as represented in available collections*

Grade Size (mm)	Dover Shale Partings N = 679 Per cent	Lower Dry Shale N = 963 Per cent	Upper Dry Shale N = 21 Per cent
32-16	0.14	0.10	----
16-8	7.03	11.20	4.80
8-4	59.60**	63.80	52.30
4-2	32.70	26.60	38.00
2-1	0.53	0.10	4.80

* Ostracods are excluded.

** A negligible number of calcareous specimens are included in these figures.

range. The following series of observations support this view: sieving sorts grains according to their least cross-sectional area (Krumbein and Pettijohn, 1938:124) which is expressed as the diameter of a sphere (Pettijohn, 1949:10). Mean and intermediate diameters are found to approach closely the value of the nominal diameter (Krumbein and Pettijohn, *op. cit.* :146 and table 15). Sieving may be used for pebbles up to 32 mm while beyond this size individual measurement is preferred (Krumbein and Sloss, 1951:71, fig. 4-2). The nominal diameter can be closely approximated by the mean diameter. The long diameter, taken alone, in the present example (table 1) is a rough approximation of the mean diameter, i.e., within a portion of one grade-size. This rough but adequate accuracy is sufficient to present an unrefined grade-size analysis for a sample of an entire fauna of the "dwarf" type. There are two reasons why this is so: first, equivalent current competence is involved in the movement of both pebbles and granules; second, the wide leeway within the respective grade-sizes, namely pebble (8.0 mm-4.0 mm, leeway of 4.0 mm) granule (4.0 mm-2.0 mm, leeway of 2.0 mm). Obviously, for problems requiring greater accuracy, nominal diameters alone should be used.

THE CONCEPT OF PSEPHONECROCOENOSIS

The general problems of dwarfism has been segmented in most previous work by the use of the biological approach (i.e., interpretation of dwarfing as due to iron, salt, phosphorus, etc.) to explain assemblages of small fossils. Such small faunas occur through much of the geologic column, but their sedimemtary and paleoecological implications have been obscured because there has been no unifying factor which could apply to *all or the majority* of such faunas. The concept of a pebble/granule necrocoenosis, as defined earlier, is proposed to serve this function.

There is a great deal of evidence to indicate that small fossil assemblages are predominantly juvenile (Tasch, *op. cit.*, Part I). It should be emphasized, however, that the possibility of growth retardation and/or the occurrence of true dwarfed individuals among fossil marine invertebrates is recognized. However, if such dwarfed adults do occur in any fauna, their presence is to be attributed to sedimentary processes such as selective bottom sorting. Thus, in the "Dry shale" fauna, several individuals of *Imitoceras grahamense* seem to be true dwarfs among a predominantly juvenile population of the same species

and a predominantly juvenile population of other species (Tasch, *op. cit.*, Part I).

Table 2 gives the results of a grade-size analysis of the entire usable sample of the Pennsylvanian "Dry shale" limonitic fauna. The iron sulfide, pyrite, oxidizes to the iron oxide limonite. Many pyritic or limonitic faunas have heretofore been referred to as "dwarf" because of the small size of all individuals. In such instances the fauna is said to be "dwarfed by iron." A similar explanation has been applied to the "Dry shale" limonitic fauna. To examine this explanation critically, table 2 was prepared. The figures given in it are based on the total number of usable fossils from a given formation. Usable fossils are defined as only those whose growth stage could be readily determined or inferred by acceptable criteria. The Dover shale partings, for example, provided a sample of 697 limonitic fossils. The grade-size analysis shows that 0.14 percent of the total sample of 697 fossils falls within the size-grade of 32.0-16 0 mm, while 7.03 percent of 697 fossils falls within the 16.0-8.0 mm grade-size, etc. In other words the bulk of the sample falls within the pebble/granule size grades. The only true dwarfs, as determined by suture spacing, were some adults of the cephalopod *Imitoceras grahamense.* Therefore, the explanation of "dwarfing by iron" cannot be applied to the entire limonitic fauna, but only to these dwarfed cephalopods. For the fauna as a whole, a non-biological explanation is needed to explain why it bulks in pebble-to-granule grade-sizes. Hence, the concept of psephonecrocoenosis is proposed.

IMPLICATIONS FOR SEDIMENTOLOGY AND PALEOECOLOGY

In each of the three shale zones shown, the major grade-size of the fossils is 8.0 mm-4.0 mm. More than ninety percent of the entire sample falls between 8.0 mm-2.0 mm. Evidently then, the detritus represented by limonitic internal fossil molds in the upper layers of the argillaceous bottom muds experienced equivalent size calibration at different times. This tells us that the competence of bottom currents was practically constant during the times represented by these shale deposits.

The association of assemblages of small fossils and oolites (Moore, 1929:471-473; 1948:126), phosphatic pellets (Ladd, 1924:1-57; 1925:1-214), and sea balls (Croneis and Grubbs, 1939:598-599) has long been known. The fact that some bottom movement is involved in the formation of oolites, pellets and sea balls strengthens the conclusion of the present paper that selective bottom sorting can explain most, if not all, such faunal assemblages. Natural sieve action, as discussed above, can account for most of the remainder. It is acknowledged, however, that there are other possibilities not considered here which may have application in special or unique instances.

Application of the concept of psephonecrocoensis to assemblages of small fossils requires a shift in emphasis in research. Biological factors are still involved, but in a different way. Sedimentary factors come to the fore. The factors to be considered when this concept is applied now include catastrophic death of an entire fauna in a given sector of the sea (Gunter, 1947:669-676), high seasonal mortality of the young of different species, and nature, extent and variability of selective bottom sorting, etc. The ecological relationship prevailing in a given sector of a sea, as indicated by lithologic and faunal evi-

dence, can, when reconstructed from such data, yield information on these factors. Thus, for example, the fact that phosphate pebbles and pellets are found in the same beds as the so-called "depauperate" fauna of the Maquoketa provides an important clue to selective sorting or bottom movement. Heretofore the presence of phosphate in these beds has been interpreted as a possible cause of depauperization. However, a search of the literature reveals no biological evidence that high concentrations of calcium phosphate in the present oceans leads to depauperization of marine invertebrates (Tasch, *op. cit.*, Part II). It follows then, that in this instance it is more fruitful to take a non-biological approach to the presence of phosphate than to maintain the traditional biological approach and ascribe unsubstantiated growth-retarding effects to it. The non-biological approach simply means that phosphate is viewed as part of the sediments. Its mode of occurrence as pebbles and pellets, then, has sedimentary significance bearing on bottom movement.

The occurence of assemblages of diminutive fossils that have been pyritized and later oxidized to limonite, as noted earlier, has usually been interpreted to be evidence of "dwarfing by iron." How, then, can "normal" or larger than normal pyritized fossils be explained? Here is where the merger of biological and sedimentary research can come about. It has been shown that the physiologically effective form of iron is *ionic iron* and that organic matter in sea water has a buffer effect (*Pufferwirkung*) on iron. Non-ionic (particulate) iron in any given sector of the sea is physiologically ineffective regardless of quantity. Similarly, high concentrations of ionic iron will also be physiologically ineffective when a sufficient amount of organic matter is present to act as a buffer (Hopkins, 1934:209-239; Uspenski, 1927:1-93). Where ionic iron can be shown to have caused growth retardation (as in the case of *Imitoceras grahamense*) the implication is that there was not enough organic matter to have a buffer effect. Where pyritic fossils of "normal" size occur, the implication is that the amount of organic matter present was sufficient to block the physiological effects of ionic iron and so permit normal growth. Thus both small and large pyritized or limonitic fossils can be indicators of organic matter in the sediments containing them. Quantities can then be determined by chemical analysis.

Further, catastrophic death of an entire fauna in a sector of the sea may imply that the area was a feeding ground. That such catastrophe did occur can be determined by lithologic and faunal evidence.

High seasonal mortality of the young of different marine invertebrate species can be determined by study of growth stages within fossil faunas. Thus, for the ammonoid *Gonioloboceras goniolobum*, it has been shown (Tasch, *op. cit.*, Part II), that juveniles, as determined by suture curvature, constituted the dominant element wherever the species has been reported. The different areas and formations involved are: Kansas (Dry shale), Missouri (shale overlying Elmo coal), Texas (Wayland shale, Finis shale), Oklahoma (Nelly Bly formation). At varying times then, in areas covered by Pennsylvanian seas, there appears to have been a high seasonal mortality of the young of this species. This suggests that such areas had become fouled. Large amounts of protoplasmic decay would enrich the sediments in organic matter. Regional studies in which information of this type is correlated with lithologic, stratigraphic, and other kinds of evidence could prove revealing.

The concept of psephonecrocoenosis, when applied to actual instances, such as those illustrated above, can release the investigator's energies for pursuit of answers which may have an important bearing on oil exploration and can certainly enhance our understanding of the rock record.

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An Ecological Study of the Microbenthic Fauna of Two Minnesota Lakes*

Gerald A. Cole

University of Louisville, Louisville, Kentucky

This report is based on a general study of a neglected and poorly-known ecological group, the lacustrine microbenthos. The microbenthos may be defined as the whole assemblage of microscopic organisms living within and on the surface of the bottom sediments. Further definition is based on limnological sampling procedure, the microbenthos being that part of the bottom community which is not retained by the coarse metal screens used in ordinary bottom-fauna studies. In this sense the microbenthos is analogous to the nannoplankton, while the macroscopic bottom animals, collectively termed macrobenthos, are analogous to the net plankton.

Results of the only previous detailed and intensive ecological study concerned primarily with the microbenthos were published by Moore (1939). His paper included an historical bibliography to which should be added at least the papers of Imel (1915), Berg (1938), and Lindeman (1941).

The data for the present paper were obtained from two Minnesota lakes. Twelve collections were made in the north arm of Lake Itasca, Clearwater County (R 36 W, T 143 N) during July and August, 1948. Eighty-six benthic collections were made from midwinter, 1948, to midsummer, 1949, in Crystal Lake, Hennepin County (R 21 W, T 29 N, Section 15). Of the total collections, 55 were qualitative, involving 73 ooze-sucker samples, and 43 were quantitative, based on 112 core samples. The molluscs, insects, malacostracans, and larger annelid worms were noted when found, but were considered macroscopic and beyond the realm of this investiagtion.

Special emphasis was placed on species distribution with respect to physicochemical factors in the lacustrine environment throughout the seasons. An appraisal of the relationships of the microbenthic assemblage to other lake biota was attempted by examining occasional plankton samples and correlating them with data from bottom collections.

Methods.—An ooze sucker (fig. 1) was built for qualitative sampling of organisms living in the upper layers of the bottom deposits. It differed from those used by Rawson (1930) and Moore (1939), although the principles

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* Based on a portion of a thesis submitted to the Graduate Faculty of the University of Minnesota in partial fulfillment of the requirements for the degree of Doctor of Philosophy.
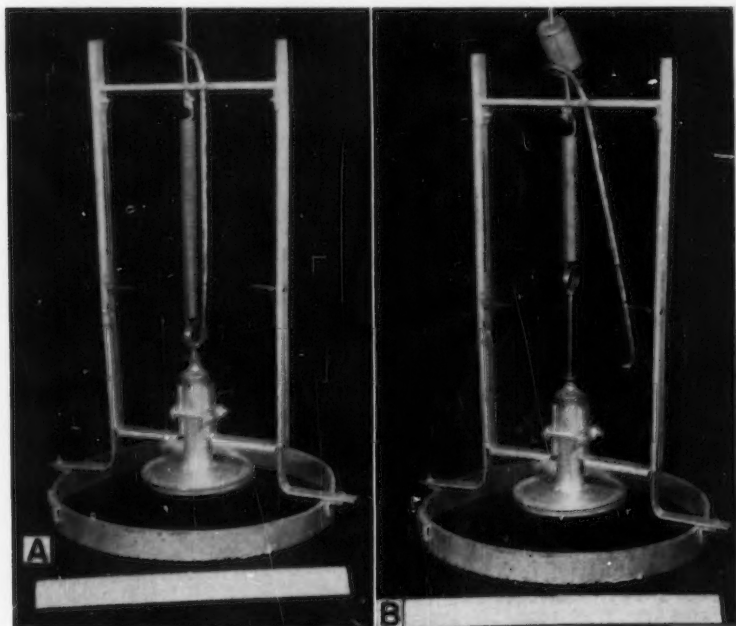
Fig. 1. Ooze Sucker.—A. Trigger mechanism cocked; B. Trigger mechanism released by messenger on line. In both pictures a 12″ rule is in the foreground

involved in its action were similar. A cylindrical metal syringe was held in a frame in such a way that, at the release of a trigger mechanism, a coil spring pulled up a piston, sucking sediment through a valve into the syringe cavity. Although not adequate for quantitative analyses, the ooze sucker served to supply good qualitative data concerning populations in the sampled areas.

For quantitative sampling of the microbenthos a small vertical core sampler was employed. A transparent plastic tube, or core liner, was fitted inside the sampler for each collection. The core liner was 60 cm long and had an inside diameter of 2.2 cm. Difficulty in retaining soft mud cores within the sampler was overcome by pushing a rubber-tipped piston into the lower end of the plastic tube before raising the core sampler from the water. The tubes with their included cores of sediment were held upright in a wooden frame after collecting and during transport to the laboratory. Each core was sectioned so that the following strata were isolated: 0-1 cm, 1-2 cm, 2-3 cm, 3-4 cm, 4-5 cm, 5-6 cm, 6-8 cm, 8-10 cm, 10-15 cm, and 15-20 cm. Usually 4 core samples were taken at a given locality. Sediments from identical strata were consolidated and diluted to 100 ml with tap water. The thoroughly-mixed material was removed one ml at a time and placed in a Sedgwick-Rafter counting cell. Five ml of the entire mixture was examined in the counting cell. The remaining material was screened with an 80 mesh Tyler screen, and examined with the aid of a low power binocular microscope. Thus, all of the larger, and one

twentieth of the smaller organisms were counted, and converted to numbers per square decimeter of bottom surface. Examination of cores revealed that the Protozoa, Gastrotricha, and Rotatoria were confined to the upper strata. For this reason all sediment below the 5-6 cm level was screened with the 80 mesh sieve before counting.

Determinations of dissolved oxygen, alkalinity, free CO_2 and pH values were made at regular intervals according to methods outlined in *Standard Methods for the Examination of Water and Sewage*, 9th edition. Sulfate, chloride, phosphorus and nitrogen values were supplied by Dr. Moyle. A Secchi disc was employed in establishing transparency, and water temperatures were measured with a standardized Taylor maximum-minimum thermometer.

Crystal Lake.—Crystal Lake is a small body of water lying northwest of Minneapolis in the city of Robbinsdale. The depression which it occupies is composed of a thin sheet of young gray till at the southern half, and of gray outwash gravel of the young gray drift at the northern half (Sardeson, 1916). There are no outlets from the lake and storm sewers serve as the only inlets.

Subsequent dredging operations have greatly modified the morphometric details of Crystal Lake, but at the time of this study the lake had a total area of 28.4 hectares. The maximum length was 780 M, and the maximum breadth was 540 M. The maximum depth was 12.5 M. The shoreline was 2.78 km, with a shore development index of 1.47. The volume was 1,172,228 cubic meters, and the volume development was 0.99. There was an annual fluctuation in water level of about a meter.

The benthic zones in Crystal Lake are here designated on the basis of their well-defined summer limits. The lakeward limit of the rooted macrophytes, 1.75 M, was considered the boundary between littoral and sublittoral zones. The upper limit of the midsummer hypolimnion was at 5 M, representing the line between the sublittoral region, and the profundal zone.

Most of the bottom collections were taken along one transect, although a few littoral samples were made off the transect to include different bottom types. In all parts of the lake deeper than 4 M the bottom types were found to be essentially uniform, and were classed as sapropel (in the sense of Lauterborn, 1901). This sediment was a putrid, soupy, black muck. At 3 M the deposits were slightly browner, but also fell into the sapropel category. In vertical section the first ten or twelve centimeters of the sapropelic ooze of the sublittoral and profundal depths were much the same. Below 15 cm the sediments were dark brown, consisting of a gelatinous mass of compacted coprogenous material (chironomid and oligochaete fecal balls). This was evidently gyttja, and much less finely divided than was the watery black sapropel which showed little evidence of coprogenesis.

At depths of 2.5 to 1.5 M along the transect the bottom deposits were dark brown, and composed of coarse plant fragments, gastropod shells, and a conspicuous coprogenic element. The term gyttja was applied to these sediments, even though much of the fine black material which composed the sapropel in the deeper parts of the lake was present at 2.5 M, and the distinction between sublittoral and profundal bottom types in Crystal Lake was not great.

The sediments at a depth of one meter were composed of blackened plant fragments, a sparse coprogenous element, mollusc shells, and more sand than seen in lakeward deposits. The material was firmer and blacker than at 2 M,

appearing to be of the sapropel series although different from the slimy sediment of the profundal and deeper sublittoral areas. Because of the contribution of the pondweeds to these deposits, the term, plant-sapropel, was applied to them.

South of the sampling transect, at depths of less than one meter, there was a firmly-packed sandy substrate, covered with a dense growth of *Chara*. The upper two centimeters of this sand was clean and light yellow in color. Below this it was blackened, and contained a few coarse pebbles.

At the south end of the lake there was a marl bottom, completely devoid of macrophytes, and supporting only a sparse fauna. This was included within the littoral area.

Crystal Lake is best described as one of the "hard carbonate" lakes of Minnesota, which lie in deposits of glacial drift, and are rich in soluble minerals (Moyle and Hotchkiss, 1945). Table 1 serves to give an overall picture of the lake as a hard, fertile body of water, reflecting in its high concentration of chloride ion a rather significant degree of pollution.

Seasonal contrasts in the physico-chemical properties of Crystal Lake were extreme during 1948 and 1949, both summer and winter periods of stagnation being lengthy. For more than half the year the deeper profundal bottom was overlain by stagnant, anoxic water, giving off a strong hydrogen sulfide odor, and containing ammonia, and a concentration of free CO_2 often in excess of 35 ppm.

The temperature of the epilimnion during summer stratification was about 25° C, the hypolimnion at the same time being about 13° C. The thermocline was usually between 4 and 5 M. In winter the water below 8 M was 4° C. There was a thick ice and snow cover, accounting for the winter stagnation conditions below 7 M.

Maximum transparency, as determined by Secchi disc readings when the

TABLE 1.—A comparison of Crystal Lake with the "hard carbonate lake" of Moyle and Hotchkiss (1945)

| Chemical factors* | Hard Carbonate Lake | | Crystal Lake | |
	Surface water Summer	Surface water February	2 m. Sept.	9 m. Sept.
SO_4 ion	0-10	30.00	14.00	0
Cl ion	less than 5	15.6	10.81	2.30
Total P	0.03-0.08	00.16	0.10	1.40
Total N	0.3-1.0	2.46	0.526	15.564
Total alkalinity	40-200	167.50	120.00	227.50
pH	8-8.8	7.2	8.4	6.8
Soluble P			0.015	1.20
Organic P			0.085	0.20
NH_3-N			0.05	8.0
NO_2-N			0.008	0.004
NO_3-N			0.100	0.20
Organic N			0.368	7.36

* Except for pH, all values expressed in ppm.

lake was open, was in the spring (52 cm). Minimum readings were obtained in the summer months, the lowest being 32 cm.

Lake Itasca.—Lake Itasca occupies a depression in the young gray drift which makes up a morainic belt approximately 15 miles wide in Hubbard and Clearwater counties. The lake shores are heavily wooded, and natural inlets and outlets are present. The lake is highly productive with richer and more varied flora and fauna than those of Crystal Lake.

Studies in Lake Itasca were limited to the north arm depression, and were made when the lake exhibited typical summer chemical and thermal stratification.

The maximum depth of the lake is 13 M, that of the north arm depression being 11 M. The lake has a total area of 441 hectares and a shoreline of 25.5 km. The shore development index is 3.42 and the volume index is 1.16. The mean depths of this lake and that of Crystal Lake are a little more than 4 M. The benthic zones of Lake Itasca were defined as 0-3 M, littoral; 3-8 M, sublittoral; and 8-13 M, profundal.

Except for one littoral sample, all collections were taken on a transect from the beach at the University of Minnesota Biological Station limnological laboratory northwest to the 11 M depression near the opposite shore. The bottom deposits along this transection were nearly uniform at depths greater than 2 M. They were composed of a brown gyttja layer 11 or 12 cm thick overlying a soft white marl layer. At about 22 cm this layer was replaced by a dry deposit of coarse marl pebbles. Samples on the transect in the littoral zone at depths of less than 2 M contained sand and gravel mixed with plant fragments. No sediments were encountered which seemed to belong to the sapropel series.

There are few data available concerning the water chemistry of Lake Itasca. However, alkalinity and pH values indicate it to fit the category, "hard, carbonate lake," (Moyle and Hotchkiss, 1945). The total alkalinity of the surface waters was 167 ppm, while at 10 M the concentration was 227 ppm. There was no free CO_2 normally in the summer epilimnion, and the concentration below the thermocline was no greater than 20 ppm. The thermocline was poorly defined, although no dissolved oxygen could be determined below 8 M. There was no indication of hydrogen sulfide in the water samples from the hypolimnion, nor was there evidence of significant organic pollution in this lake.

The epilimnion waters had a temperature of about 23° C during the period of this study, while the hypolimnion was about 17° C.

A Secchi disc reading during the first week of August, 1948, was recorded as 183 cm. This was $3\frac{1}{2}$ times greater than the maximum summer reading in Crystal Lake.

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A LIST OF MICROBENTHIC FAUNA FROM
CRYSTAL LAKE AND LAKE ITASCA

</div>

In the following list certain data are indicated after the name of each organism. The abbreviations used are: Cr, Crystal Lake; It, Lake Itasca; L, littoral; SL, sublittoral; P, profundal.

When the symbols for sublittoral and profundal are included in parentheses, it means the organism was not collected in the benthic zone indicated except during the overturn periods, or in winter months when dissolved oxygen

reached greater depths than during summer stagnation. The total number of collections in which the organisms appeared is recorded last in parentheses.

PROTOZOA

Anisonema sp.	Cr; L, (SL), (P);	(7)
Astasia klebsi Lemmermann	It; P;	(1)
	Cr; L, SL, P;	(31)
Bodo sp.	Cr; P;	(3)
Ceratium hirundinella (Müller)	It; L;	(1)
Chilomonas paramecium Ehrenberg	Cr; L, SL, P;	(9)
Chlamydomonas sp.	Cr; L;	(1)
Cryptomonas sp.	Cr; L;	(2)
Distigma proteus Ehrenberg	Cr; L;	(1)
Entosiphon sp.	Cr; L;	(2)
Euglena sp.	Cr; L, SL, (P)	(6)
Heteronema sp.	Cr; L;	(1)
Lobomonas sp.	Cr; L;	(1)
Mallomonas sp.	Cr; L;	(2)
Menoidium incurvum (Fresenius)	Cr; L, SL, P;	(9)
Menoidium sp.	Cr; P;	(3)
Monas sp.	Cr; L, P;	(6)
Peranema sp.	Cr; SL;	(1)
Peridinium sp.	Cr; L;	(4)
Petalomonas sp.	Cr; L, SL, (P);	(4)
Phacotus lenticularis (Ehrenberg)	Cr; L, SL, P;	(42)
	It; L, P;	(2)
Pleuromonas sp.	Cr; L;	(2)
Scytomonas sp.	Cr; L;	(1)
Trachelomonas volvocina Ehrenberg	Cr; L, SL, (P);	(15)
Unidentified flagellates	It; L, SL, P;	(6)
	Cr; L, SL, P;	(46)
Amoeba sp.	Cr; L, SL, (P);	(3)
Arcella vulgdris Ehrenberg	It; L;	(2)
Pelomyxa palustris Greeff	It; SL, P;	(2)
	Cr; P;	(2)
Vahlkampfia limax (Dujardin)	Cr; (P);	(1)
Aspidisca costata Dujardin	Cr; L, SL, (P);	(6)
Blepharisma sp.	Cr; L;	(2)
Chilodonella sp.	Cr; L, (SL), (P);	(7)
Cinetochilum margaritaceum Perty	Cr; (SL), (P);	(5)
Codonella cratera (Leidy)	Cr; L;	(1)
Coleps hirtus (Müller)	It; P;	(1)
	Cr; L, SL, (P);	(19)
Colpoda sp.	Cr; (SL), (P);	(4)
Cyclidium sp.	Cr; L;	(1)
Didinium nasutum (Müller)	Cr; (SL);	(1)
Dileptus anser (Müller)	Cr; L;	(1)
Epistylis sp.	Cr; SL;	(1)
Euplotes sp.	Cr; L;	(1)
Frontonia leucas Ehrenberg	Cr; L, SL, P;	(6)
Halteria grandinella (Müller)	Cr; L, (P);	(3)
Lembadion bullinum Perty	Cr; L;	(1)
Lionotus sp.	Cr; L;	(3)
Loxodes sp.	It; L, SL, P;	(3)
	Cr; L;	(4)
Loxophyllum sp.	Cr; (SL);	(1)
Metopus es Müller	Cr; L, SL, (P);	(7)
Metopus sp.	Cr; L, SL, P;	(7)
Nassula sp.	Cr; SL, P;	(3)
Paramecium caudatum Ehrenberg	Cr; SL, P;	(3)

Protozoa (continued)

Rhagadostoma sp.	Cr; SL, P;	(15)
Spirostomum minus Roux	Cr; P;	(1)
Spirostomum teres Claparédè and Lachmann	Cr; L, (P);	(4)
Stentor roseoli Ehrenberg	Cr; (SL), (P);	(2)
Stylonichia sp.	It; L;	(1)
	Cr; L;	(3)
Vorticella sp.	Cr; L, SL, (P);	(20)
Unidentified ciliates	It; L, SL;	(3)
	Cr; L, SL, P;	(40)
Podophrya sp.	Cr; L;	(1)

Rhabdocoelida

Dalyellia viridis (G. Shaw)	Cr; L;	(1)
Dalyellia sp.	Cr; L;	(1)
Gyratrix hermaphroditus hermaphroditus Ehrenberg	It; L;	(2)
	Cr; L;	(3)
Microstomum sp.	It; L;	(1)
	Cr; L;	(1)
Unidentiled Rhabdocoelida	It; SL	(1)
	Cr; L;	(7)

Nematoda

Dorylaimus sp.	It; L, SL;	(2)
Trilobus sp.	Cr; SL, P;	(34)
Unidentified Nematoda	It; L, SL, P;	(10)
	Cr; L, SL, P;	(26)

Rotatoria

Dissotrocha macrostyla (Ehrenberg)	It; L;	(1)
	Cr; L;	(4)
Diurella tigris (Müller)	Cr; L;	(1)
Euchlanis sp.	Cr; L;	(3)
Keratella cochlearis (Gosse)	Cr; L;	(4)
Lecane luna (Ehrenberg)	It; L;	(1)
	Cr; L;	(2)
Polyarthra trigla (Ehrenberg)	It; L;	(1)
	Cr; L;	(1)
Rotaria neptunia (Ehrenberg)	Cr; L, SL;	(6)
Rotaria rotatoria (Pallas)	It; L;	(1)
	Cr; L, SL, P;	(15)
Synchaeta sp.	It; L;	(1)
	Cr; (SL), (P);	(2)
Unidentified Rotatoria	Cr; L;	(2)

Gastrotricha

Chaetonotus sp.	It; P;	(1)
	Cr; L, SL, (P);	(14)

Oligochaeta

Aeolosoma hemprichi Ehrenberg	Cr; L;	(1)
Aelosoma sp.	It; L.	(3)
Chaetogaster pellucidus Walton	Cr; L;	(1)
Chaetogaster sp.	It; L;	(2)
	Cr; L;	(1)
Dero sp.	Cr; L;	(1)
Naidium sp.	It; L;	(3)
	Cr; L;	(3)
Nais sp.	It; L;	(1)
	Cr; L;	(3)
Stylaria lacustris (Linnaeus)	It; L;	(2)
Unidentified Oligochaeta	It; L;	(2)
	Cr; L;	(3)

CLADOCERA

Alona affinis (Leydig)	It; L;	(2)
Alona quadrangularis (O. F. Müller)	It; L;	(3)
	Cr; L;	(2)
Alona rectangula Sars	Cr; L;	(1)
Alona sp.	It; L;	(4)
Alonella excisa (Fischer)	It; L;	(1)
Alonella rostrata (Koch)	It; L;	(1)
Alonella sp.	It; L;	(2)
Bosmina longirostris (O. F. Müller)	Cr; L, (SL), (P)	(8)
Camptocercus rectirostris Schoedler	Cr; L;	(1)
Ceriodaphnia quadrangula (O. F. Müller)	Cr; L;	(1)
	It; L;	(1)
Chydorus sphaericus (O. F. Müller)	Cr. L;	(2)
	It; L;	(2)
Daphnia longispina (O. F. Müller)	Cr; L, (SL), (P);	(7)
	It; L;	(1)
Daphnia pulex (de Geer)	It; L;	(1)
Diaphanosoma brachyurum (Liéven)	It; L, SL;	(2)
Drepanothrix dentata (Eurén)	It; L;	(1)
Ilyocryptus sordidus (Liéven)	It; L;	(4)
	Cr; L, SL;	(9)
Ilyocryptus spinifer Herrick	It; L;	(2)
Latona setifera (O. F. Müller)	It; L;	(1)
Leydigia quadrangularis (Leydig)	It; L;	(1)
	Cr; L, SL;	(9)
Macrothrix laticornis (Jurine)	Cr; L, SL, (P);	(11)
Pleuroxus denticulatus Birge	It; L;	(1)
Pleuroxus trigonellus (O. F. Müller)	It; L;	(1)
Scapholeberis mucronata (O. F. Müller)	It; L;	(1)
Simocephalus serrulatus (Koch)	It; L;	(1)
Simocephalus vetulus (O. F. Müller)	It; L;	(1)

COPEPODA

Attheyella bidens coronata (Sars)	It; L;	(1)
Canthocamptus sp.	It; L;	(2)
Cyclops bicuspidatus thomasi S. A. Forbes	Cr; L, SL, P;	(56)
Cyclops vernalis Fischer	It; L;	(1)
Diaptomus oregonensis Lilljeborg	It; L;	(1)
Diaptomus pallidus Herrick	Cr; L, (P);	(3)
Eucyclops agilis (Koch)	It; L;	(2)
	Cr; L, SL, (P);	(8)
Macrocyclops albidus (Jurine)	It; L;	(2)
Mesocyclops edax (S. A. Forbes)	It; L, SL;	(2)
	Cr; L, SL, P;	(32)
Paracyclops fimbriatus (Fischer)	It; L;	(2)
Immature Copepoda	It; L;	(7)
	Cr; L, SL, (P)	(20)

OSTRACODA

Candona fluviatilis Hoff	It; L;	(2)
Candona simpsoni Sharpe	It; L;	(2)
	Cr; L;	(1)
Candona sp.	It; L, SL;	(3)
	Cr; L, SL;	(3)
Cypria turneri Hoff	It; L, SL;	(5)
	Cr; L, SL, P;	(10)
Cypridopsis vidua (O. F. Müller)	It; L;	(3)
	Cr; L;	(1)
Darwinula stevensoni (Brady and Robertson)	It; L, SL;	(5)
Limnocythere itasca Cole	It; L;	(6)
Physocypria pustulosa (Sharpe)	It; L, SL;	(6)

OSTRACODA (continued)

	Cr; L, SL, P;	(5)
Potamocypris smaragdina (Vavra)	It; L;	(1)
	Cr; L;	(1)
Unidentified Ostracoda	It; L;	(1)
	Cr; L, SL;	(2)

ACARINA

Nymphal mites	It; L;	(4)

TARDIGRADA

Macrobiotus sp.	Cr; L;	(1)

PATTERNS AND SEASONAL FLUCTUATIONS OF
MICROBENTHIC POPULATIONS

Thermal and chemical stratification of Crystal Lake during the summer months brought about a sharp definition of benthic regions unequalled at other times.   Apparently in response to physico-chemical factors the distribution patterns of animal species down the basin slope also were defined most clearly in summer.

Most taxonomic groups were represented by more species in littoral collections than in those from sublittoral and profundal zones.   This was due in part to the unique position of the littoral benthic community in relation to two other major communities: the plankton, and the organisms living among the aquatic macrophytes near the lake margin.   Many species which are not truly bottom forms were included in littoral samples.   Several were obvious plankters (e.g. *Ceratium, Codonella, Keratella, Polyarthra, Diaptomus*), and probably many of the littoral cladocerans were more typically weed-dwelling forms. However, of the species believed to be truly benthic, the greatest numbers were collected from littoral sediments.   The Rhabdocoelida and Naididae were apparently confined to that region in Crystal Lake, and most of the Protozoa, rotifers, Cladocera, and ostracods were littoral.   Several species occurred only in littoral areas during the summer, but were found in deeper regions during overturn periods and the winter months (e.g. *Chilodonella, Halteria, Spirostomum*).

The littoral sediments of Crystal Lake were more varied than those farther lakeward, and the benthos was by no means uniform in shallow water.   Of the three main types of littoral bottom, the plant-sapropel supported the greatest number of species.   This was apparently the most favorable substrate from a trophic standpoint.   Furthermore, the population here was three dimensional, including several burrowing species found less commonly on other bottom types.   *Candona*, a burrowing ostracod, was not found on the firmly-packed sand, nor on the marl bottom, while the nematode worms, oligochates, and *Ilyocryptus sordidus* were far more abundant in the plant-sapropel sediments than in the other types.   For example, midsummer quantitative collections showed there to be about 342 *Ilyocryptus* individuals per square decimeter in the plant-sapropel as compared with about 13 and 9 in the sand and marl respectively.   The sand bottom had about half the number of species found on plant-sapropel, but twice as many as were present on the clean marl bottom. Several species were found only on sand bottoms, the rotifers, *Euchlanis* and *Dissotrocha*, being good examples.   No animals penetrated below 2 cm in this material.

The sublittoral zone of Crystal Lake during summer was characterized mostly by species which occurred more abundantly in either littoral or profundal regions. The benthic cladocerans, *Ilyocryptus sordidus* and *Leydigia quadrangularis* were considered littoral species, but they were occasionally collected in sublittoral samples. The same was true for the burrowing ostracod, *Candona*, and *Macrothrix laticornis*, a cladoceran capable of swimming, but usually found near the bottom. A nematode of the genus *Trilobus*, and encysted *Cyclops bicuspidatus thomasi* were common profundal forms which were found in deep sublittoral depths in greatly reduced numbers. Only *Mesocyclops edax* and *Cypria turneri* were considered typical of the sublittoral zone, occurring there in greater numbers than in littoral sediments. At times *M. edax* was the only metazoan found in collections halfway down the sublittoral slope at three M. In Lake Itasca it was common at the comparable sublittoral depth of 5 M, but in each lake the greatest portion of the population during summer was in the plankton.

Of 34 bottom samples in which *Mesocyclops edax* occurred only 4 included adult males, the typical specimen being a mature female. The males were also scarce in the plankton collections, further evidence for a differential sex ratio in this species as reported by Kofoid (1908).

The anoxic hypolimnion waters of Crystal Lake presented an aggregation of environmental factors which was evidently unfavorable for most bottom forms. Oligochaetes and Sphaeriidae were never collected in the profundal zone, while chironomids and *Chaoborus* larvae were extremely rare. *Trilobus* sp., *Rotaria rotatoria*, and active and encysted *Cyclops bicuspidatus thomasi* in the 4th copepodid stage were the only metazoans occurring there in significant numbers. *Rotaria* was a member of the microbenthic population at all depths in the lake, but *Trilobus* and encysted *Cyclops* were never found farther up the basin slope than sublittoral depths very close to the boundary between epilimnion and hypolimnion. *Trilobus* numbers decreased as summer stagnation progressed. In early summer (the last of May) there were about 120 *Trilobus* per square decimeter at 6 M as compared with about 80 and 26 at 9 M and 12.5 M, respectively. By the middle of July the numbers had fallen to about 7 per square decimeter at 12 M, and roughly 50 or 60 at 6 M and 9 M. On the other hand, the cysts of *Cyclops* increased in numbers as the summer progressed. This increase corresponded roughly to the decrease in numbers of active immature individuals in the sediment. The cyst population during 1948 was much larger than in 1949, but each year the greatest numbers were at medium profundal depths as contrasted to the Douglas Lake population, where the most cysts were in the deepest part of the lake (Moore, 1939). In 1949 the greatest numbers calculated per square decimeter were about 8,800 at 9 M and about 6,000 at 6 M and 12 M. There was an apparent decrease in cysts at 6 M from early June to the middle of July. This decrease of about 2,000 per square decimeter may have been due to *Chaoborus* predation, for a small population of *Chaoborus* was present at that depth during the period of decline, and none were found at deeper stations where the cysts increased. The cysts were present below 15 cm in the ooze, but more than half were at the surface or in the upper centimeter of profundal sapropel. Throughout the greater part of the summer the entire *Cyclops bicuspidatus thomasi* population was benthic and in the 4th copepodid state (table 2).

The Protozoa of the summer profundal zone were not peculiar to that region, with the possible exception of *Pelomyxa palustris,* not collected at other levels in Crystal Lake. In Lake Itasca this species was found in both pro-fundal and sublittoral collections.

Chilomonas paramecium, Astasia klebsi, Phacotus lenticularis, and tiny unidentified flagellates were by far the most abundant of the profundal proto-zoans, but were present at all depths in the lake. *Chilomonas* was easily iden-tified in littoral collections, but in the sublittoral and profundal sapropel it assumed an unusual form. There the cell was plastic, and the starch granules were either clumped at the anterior end, or at both ends with the central region clear. Dr. Kenneth L. Osterud has informed me that he has found the same abnormal type of *Chilomonas* in sewage. *Phacotus* was the only green flagel-late found regularly in the anoxic hypolimnion, where it must have existed in almost complete darkness. It was a common member of the plankton com-munity also.

Of the ciliates, *Rhagadostoma* sp., was the hardiest with respect to stagna-tion endurance in Crystal Lake. It outlasted such genera as *Coleps, Parame-cium* and *Metopus,* but showed a marked decline in numbers as stagnation progressed. Interestingly, this abundant ciliate was never found in littoral samples. Single specimens of *Nassula,* and *Spirostomum minus* were taken in stagnant profundal collections.

The summer profundal community of Lake Itasca was richer in species than that of Crystal Lake. The most obvious factors accounting for this dif-ference are the general pollution, the production of H_2S, and the long periods of stagnation in Crystal Lake. *Coleps hirtus, Loxodes* sp., *Metopus* spp., and

TABLE 2.—Seasonal and vertical distribution of *Cyclops bicuspidatus thomasi* in the sublittoral and profundal sediments of Crystal Lake

Depth in cm	Adult	Immature	Cyst	Adult	Immature	Cyst	Adult	Immature	Cyst	Adult	Immature	Cyst
						Number per 10 cores						
0-1	0	136.0	0	15.0	3.8	0	0	67.5	1.3	0	49.9	1,859.3
1-2	0	104.0	0	0	0	1.3	0	10.0	0	0	5.8	564.8
2-3	0	78.0	0	0	0	0	0	1.3	0	0	2.5	88.3
3-4	0	48.0	0	0	0	0	0	1.3	0	0	.8	66.6
4-5	0	84.0	0	0	0	0	0	1.3	0	0	.8	39.9
5-6	0	10.0	0	0	0	0	0	2.5	0	0	0	24.9
6-8	0	10.0	0	0	0	0	0	5.0	0	0	1.7	29.9
8-10	0	10.0	0	0	0	0	0	2.5	0	0	0	9.9
10-15	0	8.0	0	0	0	0	0	2.5	0	0	0	3.3
15-20	0	14.0	0	0	0	0	0	0	0	0	0	.8
	Late Winter			Spring Overturn[1]			Late Spring[2]			Early Summer[3]		
	3/7/49-3/24/49			4/26/49-4/29/49			5/10/49-5/17/49			5/26/49-5/30/49		

[1] Plankton—Ovigerous adults abundant 4/16, 4/22.

[2] Plankton—Immature abundant; adults rare 5/7, 5/21.

[3] Plankton—All stages rare 6/5.

many minute, unidentified ciliates were present in the anaerobic waters of Lake Itasca. The gastrotrich, *Chaetonotus*, was also common in profundal sediments of Itasca, but did not appear in anaerobic collections from Crystal Lake. Furthermore, the profundal nematodes and the macrobenthic insect larvae and oligochaetes were much more abundant in Lake Itasca.

As the fall overturn began in Crystal Lake, the termination of stagnation could be traced down the profundal slope by reference to the biota alone. The impoverished summer population became enriched by the appearance of species not seen since spring at profundal depths. Meanwhile, in the sediments below the descending thermocline, the benthos retained its summertime aspect.

By the first week in October the lake was practically homothermous, and core samples taken from the deepest regions revealed many new forms. These included the crustacean plankters, *Daphnia longispina, Bosmina longirostris, Diaptomus pallidus, Mesocyclops edax*, and *Eucyclops agilis*. The last species was considered typical of the littoral zone during the summer months, never being found in the deep sublittoral, or the profundal sediments. With the exception of *Cyclops bicuspidatus thomasi*, and *Mesocyclops edax*, the occurrence of Copepoda and Cladocera on the profundal bottom was extremely brief, coinciding with the first few days of complete circulation, although dissolved oxygen was present there well into the winter. *Cyclops bicuspidatus thomasi* began to excyst in late summer before the overturn, and adults were found throughout the lake during the period of free circulation. However, many cysts remained in the sediments until January, and this species was not a conspicuous element of the fall plankton.

With the removal of stagnation conditions during the fall overturn several ciliates appeared in the profundal sediments. *Coleps hirtus, Frontonia leucas, Chilodonella* sp. and *Rhagadostoma* sp. made up the greatest part of this population.

Following the formation of the winter ice cover, water below 7 M became anoxic. The ciliate population was greatly reduced, although *Rhagadostoma* survived in significant numbers. The copepod, *Mesocyclops edax*, no longer occurred in the deepest regions, but was collected in diminishing numbers down the lake basin until anaerobic water was reached. There were approximately 260 square decimeter at a depth of 2.25 M, 210 at 4.75 M and 180 at the boundary of aerobic and anaerobic bottom near 7 M. None were found below this line. These animals burrowed as far down as the 10-15 cm stratum, although about half of the population was in the uppermost stratum (0-1 cm).

By late winter all the *Cyclops bicuspidatus thomasi* were excysted and the sediments at every depth contained many active individuals, burrowing to a depth of more than 15 cm in the soft deposits (table 2). The pattern of distribution down the basin slope differed from that of *M. edax*, the animals increasing numerically with depth. Most of them were in the deepest part of the lake in anaerobic water. Core-sample analyses revealed approximately 80 *Cyclops* per square decimeter at 2.25 M, 240 at 4.75 M, 1,300 at 7 M, 1,500 at 9.5 M, and more than 3,700 at 12.5 M. Although emerged from the cyst and active, these copepods were still in the 4th copepodid stage.

The spring overturn brought about a tremendous change in the microbenthos, the enrichment of the profundal and sublittoral fauna with many ciliate

species being the most conspicuous feature. Several species were seen only at this time and were extremely abundant for a brief period (e.g. *Cinetochilum margaritaceum, Stentor roseoli*).

At the same time, the entire *Cyclops bicuspidatus thomasi* population rapidly underwent the two moults necessary for the attainment of maturity, and left the sediments. They became the predominant species in the spring plankton. Core samples taken early in May, 1949, contained no representatives of this species, there probably being a brief time when the entire population was pelagic and reproductively active. By the end of the first week in May most of the new generation had passed through 6 naupliar and three copepodid stages, and had attained the 4th copepodid stage. The immature specimens then dominated the plankton, and adults were rare. Before the middle of May many of the young copepods migrated to the benthic niche, although a few lingered in the plankton. By early June plankton hauls took no members of this species; only immature specimens were present in the lake, and these were all benthic and in the 4th copepodid stage (table 2).

Apparently most *Mesocyclops edax* also left the sediments at the overturn, and those that remained no longer burrowed deep in the bottom deposits. At this time, and during the summer months, analyses of many cores revealed only one individual as deep as the 2-3 cm stratum, and more than 90% were at the ooze surface or in the top centimeter. Spring and summer benthic populations were much smaller than those of the winter, there usually being only 50 or 55 per square decimeter at the sublittoral depth of 3 M where the greatest concentration occurred.

The establishment of thermal and chemical stratification in early summer was attended by the disappearance of the rich, spring ciliate population. The profundal regions once more were inhabited only by those forms apparently more resistant to unfavorable factors in stagnant water, and faunal zonation down the slope of the basin became well defined. The prolongation of stagnation was accomplished by further impoverishment of the profundal microbenthos, with the only positive increase being exhibited by the new generation of encysted *Cyclops bicuspidatus thomasi* (table 2).

Vertical Distribution of Microbenthos in the Sediments

During this investigation quantitative collections made with the core sampler were sectioned in such a manner that it was possible to determine to what levels organisms penetrated the bottom deposits. This component of animal distribution has been unheeded by most workers, although Rawson (1930), Lenz (1931), Berg (1938) and Moore (1939) presented some data on vertical distribution in the sediments.

Few core samples were taken from the firm sand bottom near the east margin of Crystal Lake, but those that were examined contained no animals below the 1-2 cm stratum. Oligochaetes and chironomids as well as the microfauna were confined to the upper layer of this hard bottom, although they penetrated several centimeters into soft deposits. Moore (1939) demonstrated a similar phenomenon with respect to the nematode population in Douglas Lake, where 89.7% of the total on sand bottom were confined to the upper two centimeters, and only 63.5% were at that level in muck bottom. The sand bottom of Crystal Lake is even firmer than that of Douglas Lake.

Some of the microorganisms which were numerous throughout the year in Crystal Lake sediments were found to vary seasonally in their vertical distribution. This was true of *Cyclops bicuspidatus thomasi* (table 2), and *Mesocyclops edax*, found deeper in benthic materials during the winter months than at other times. This may have been true also for the ostracod, *Physocypria pustulosa*, and the nematode, *Trilobus* sp., but the statistical validity of the

TABLE 3.—Vertical distribution in the sediments of representative microorganisms from Crystal Lake

Depth in cm	Unidentified flagellates Estimated number	%	Phacotus lenticularis Estimated number	%
0-1	4,420	69.9	520	38.8
1-2	1,180	18.7	680	50.8
2-3	380	6.0	140	10.5
3-4	260	4.1	....	....
4-5	80	1.3	....	....
5-6	....	....	....	....
6-8	....	....	....	....
8-10	....	....	....	....
10-15	....	....	....	....
15-20	....	....	....	....
Total	6,320		1,340	
No. of Cores	28		20	
Bottom types	Soft		Soft	
Water depth in M	2.5-12.5		2.5-12.5	
Season	4/16-5/28		4/29-5/30	

TABLE 3.—(*continued*)

Depth in cm	Rhagadostoma sp. Estimated number	%	Stentor roseoli Estimated number	%	Rotaria rotatoria Estimated number	%
0-1	13,180	86.9	700	89.74	340	85
1-2	1,700	11.2	40	5.13	40	10
2-3	180	1.2	40	5.13	20	5
3-4	80	0.5	....	....	....	....
4-5	20	0.1	....	....	....	....
5-6	....	....	....	....	....	....
6-8	....	....	....	....	....	....
8-10	....	....	....	....	....	....
10-15	....	....	....	....	....	....
15-20	....	....	....	....	....	....
Total	15,160		780		400	
No. of Cores	28		8		29	
Bottom type	Soft		Soft		Soft	
Water depth in M	4.5-12.5		4.5-10.3		2.5-12.5	
Season	4/26-5/30		4/26-4/29		3/24-5/30	

TABLE 3.—(*continued*)

| Depth in cm | Trilobus sp. | | | Ilyocryptus sordidus | | |
	Actual number	%		Actual number	%
0-1	30	30.6		27	75.0
1-2	23	23.5		2	5.5
2-3	18	18.4		1	2.8
3-4	12	12.2		3	8.3
4-5	4	4.1		1	2.8
5-6	6	6.1		....	....
6-8	4	4.1		1	2.8
8-10	1	1		1	2.8
10-15	....	....		....	....
15-20	....	....		....	....
Total	98			36	
No. of Cores	43			10	
Bottom type	Soft			Soft	
Water depth in M	4-12.5			0.25-3	
Season	3/7-7/16			5/17-6/16	

data may be questioned. In table 3, a compilation based on 43 cores containing *Trilobus* throughout all seasons is shown. This serves only as a rough generalization of nematode stratification in the sapropel of Crystal Lake, with 54.1% of the population in the upper two centimeters. The seasonal aspects were different. In late winter 16.7% of those collected were in the upper two centimeters, as constrasted with 42.1% in spring, and 70.4% in the summer.

Table 3 presents information concerning stratification of several microscopic bottom animals in the sediments. The data are arranged in such a way that a composite picture of many core samples is shown for each species. The total number of cores varies from species to species, but the frequency of occurrence at each level is expressed as a percentage of the total number of individuals so that comparisons can be made.

The Protozoa were not found below 5 cm in the sediments. This was true also of the minute metazoans (e.g. *Rotaria*). Almost 70% of the small unidentified flagellates were found at the upper surface or in the uppermost centimeter of the soft sapropelic deposits. The green flagellate, *Phacotus lenticularis*, showed a somewhat different distribution, more being counted in the 1-2 cm stratum than in the layer above. Because of the difficulty in counting protozoans in the bottom deposits, the validity of the *Phacotus* data may be open to question.

Most ciliated protozoans were confined to the uppermost level even more than were the flagellates. Some species (e.g. *Chilodonella*) were not seen below the second centimeter, but in the case of the very abundant *Rhagadostoma* there were rare occurrences as far down as the 4-5 cm level. The large ciliate, *Stentor roseoli*, was observed briefly during the spring overturn in Crystal Lake, but enough individuals were collected to show a definite stratification characterized by almost 90% of the population in the uppermost centimeter. There was a striking similarity between the feeding behavior of this

protozoan and the rotifer, *Rotaria rotatoria.* The vertical distributions of the two species in the sapropel were also very similar.

Ilyocryptus sordidus was the only cladoceran which burrowed into the sediments. Although individuals were distributed down to the 8-10 cm level in soft sediments, 75% of the total population was found in the uppermost centimeter.

Generalizations can be made concerning the vertical distribution of animals in the bottom deposits of Crystal Lake. The greatest portion of the benthic fauna is restricted to the uppermost centimeter of the deposits. The vertical distribution of the fauna depends, in part, upon the nature of the sediments. Firmly-packed materials prohibit penetration more than do soft and watery deposits. Inherent specific factors are also important, and the stratification of different species in identical sediments is by no means uniform.

DISCUSSION

During the course of this study it became apparent that many species considered to be holoplanktonic or free-floating throughout life are actually closely associated with the benthic habitat. This is by no means a novel idea. Wesenberg-Lund (1908) pointed out the exchange between littoral forms and the plankton, and the origin of pelagic populations from the benthic region. Butcher (1932) concluded from a study of the microflora of streams that many organisms in the potamo-plankton are derived from benthic algal communities rising to the limnetic niche as they age. It is well known that many fluctuations in zooplankton populations are due to the return to, and the departure from the benthic niche, where life is passed in some sort of resting stage. However, plankton studies are usually somewhat abstract, in that other niches are ignored. Seasonal maxima and minima of plankton refer only to limnetic numbers, and the overall picture of the organisms in the aquatic ecosystem is not presented. The interesting resting stage of *Cyclops bicuspidatus thomasi* has been known since 1908 (Birge and Juday, 1908) although reported only once since then (Moore, 1939). This copepod is a constitutent of plankton populations and has been included in many reports on plankton (e.g. Kofoid, 1908; Eddy, 1934; Pennak, 1949). However, in Crystal Lake it is incorrect to think of it as a plankter alone, because there are long periods spent as a benthic organism. This is true to a lesser degree for *Mesocyclops edax,* which is very common in the sediments during the winter months. At the vernal overturn it leaves the deeper deposits, but is found regularly on the surface of sublittoral deposits in somewhat reduced numbers. Most of the summer population is contained in the plankton, but even at this time of year the benthic habit is strongly developed.

These data suggest that trophic relations, and cyclic phenomena linking dissolved nutrients and the biomass are not alone in indicating the unity of the lake ecosystem. The facts of ecological life histories show that the line of demarcation between benthos and plankton is, to a greater extent hazy and poorly defined.

The role of the microbenthos in the economy and trophic dynamics of the lake is not easy to evaluate in exact quantitative terms. The difficulties involved in accurately counting the smaller bottom forms or in separating them from the substrate precludes an accurate estimation of the portion of the lake

biomass which is the microbenthos. In general, the microbenthic assemblage differs from the planktonic community in two important features: there are fewer individuals, and there are relatively fewer trophic producers in the sediments than in the water of the lake. The bottom deposits are primarily a region of consumption rather than of production, with saprophagy assuming great importance. The paucity of macroscopic benthic predators in the deeper sublittoral and profundal deposits of Crystal Lake suggests that most of the truly benthic microorganisms there contribute their remains to the sediments upon death, and are not passed on directly to higher trophic levels. In the littoral areas of Crystal Lake, where there are many small fish and such benthic predators as Odonata naiads, much of the organic substance of the microbenthos is probably transferred to higher levels by predatory activity. In this region, at least, the microorganisms of the bottom deposits form a link in the food chain, leading ultimately to the larger carnivorous fish.

SUMMARY

An investigation was undertaken for the purpose of studying the benthic microfauna throughout the seasons of the year, with particular reference to the effects of physico-chemical factors within the lacustrine environment.

Eighty-six benthic collections were made from midwinter 1948 to midsummer 1949 in Crystal Lake, Hennepin County, Minnesota, and twelve collections were taken during July and August 1948 from the north arm of Lake Itasca, Clearwater County, Minnesota.

Crystal Lake showed evidence of pollution. Its sediments were largely sapropelic, and there was a conspicuous formation of H_2S during the long anaerobic periods in the deeper waters.

Lake Itasca was a highly productive lake, showing little evidence of pollution. Its sediments were largely gyttja, and no H_2S was detected in its summer hypolimnion.

A total of at least 133 species of microscopic animals were recorded from the bottom sediments of the two lakes. These consisted of: 58 Protozoa, 5 Rhabdocoelida, 3 Nematoda, 10 Rotatoria, 1 of the Gastrotricha, 9 Oligochaeta, 25 Cladocera, 10 Copepoda, 10 Ostracoda, 1 of the Acarina, and 1 of the Tardigrada.

Littoral bottoms supported the greatest number of microfaunal species, and many were confined to the one zone. *Mesocyclops edax*, and *Cypria turneri* were considered to be typical of the sublittoral zone, but occurred also in the littoral zone. *Pelomyxa palustris*, a nematode of the genus *Trilobus*, and encysted *Cyclops bicuspidatus thomasi* were the only species typical of the profundal zone, but they were not wholly confined to that region.

In Lake Itasca the sand and gravel littoral bottom had more species than the gyttja deposits farther lakeward. In Crystal Lake the soft plant-sapropel sediments near the lake margins contained more species than the sand and marl bottoms at the same depth. Several species were found to be more abundant on sand bottom than elsewhere.

Each overturn period in Crystal Lake resulted in a conspicuous qualitative enrichment of the profundal and sublittoral populations.

The vertical distribution of organisms in the sediments was studied by sectioning core samples at different levels. Most animals were in the upper

centimeter of bottom deposits, but individuals of some species were found below a level of 15 cm in the sediment.

Special attention was devoted to the organisms living in the anaerobic profundal zones of the two lakes. Smaller and less varied populations were found in the hypolimnion of Crystal Lake than in Lake Itasca.

On several occasions so-called planktonic forms were found in the benthic deposits. Many occurrences were accidental but others were due to the fact that some plankters have benthic phases in their life histories.

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Bryophyta of Arctic America. VI. A Collection From Prince Patrick Island

William C. Steere*

Stanford University, Stanford, California

While engaged in field work in arctic Canada during the summer of 1949, the well-known collector, Mr. Charles O. Handley, Jr., of the Division of Mammals of the United States National Museum, obtained an excellent series of mosses and hepatics on Prince Patrick Island. Since the bryophytes of this remote area have remained completely unknown until now, a special acknowledgment should be made to Mr. Handley for his painstaking and industrious attention to a group of organisms far removed from the center of his professional interest, the mammals. The specimens were received for identification through the courtesy of the United States National Herbarium, where the collection is now deposited.

Prince Patrick Island, the northern of the two westernmost islands of the whole Canadian arctic archipelago, is situated between the parallels of 76° and 78° N. Bisected by the 120th meridian (W. Long.), this island lies due north of Banks Island, and of Great Bear Lake on the Canadian mainland. The great majority of the specimens reported upon here were collected in the vicinity of the weather station at Mould Bay (76° 14' N., 119° 50' W.), at the southeast corner of the island, but a few are from Intrepid Inlet, which also faces the Crozier Channel scmewhat farther north. As commander of H.M.S. 'Intrepid,' one of five ships under the command of Sir Edward Belcher, Captain Leopold McClintock discovered, fully explored and named Prince Patrick Island in 1853. Although this last official expedition sent out by the British Government to search for Sir John Franklin failed in its primary mission, a later expedition under private auspices, with McClintock in command of the yacht 'Fox,' finally solved the mystery of the disappearance of Franklin and his ships (McClintock, 1859).

The rigors of life and travel in arctic America prevented most of the early explorers from making botanical collections, especially of lower plants, and no bryophytes at all seem to have been known from Prince Patrick Island prior to Mr. Handley's visit, a circumstance that adds unusual importance to his collection. As will be seen from the following catalogue of 5 species of hepatics and 93 of mosses, Handley's collection adds very considerably to our knowledge of the geographical distribution of bryophytes in northernmost America, filling in a previously unknown western segment of the Canadian arctic archipelago. Species of especial significance in this collection, as representing major extensions of geographic range, are: *Aulacomnium acuminatum, Barbula icmadophila, Bryobrittonia pellucida, Ceratodon heterophyllus, Cinclidium latifolium, Ctenidium molluscum, C. procerrimum, Desmatodon leucostomus, Distichium hageni, Drepanocladus lycopodioides, Hygrohypnum polare, Pottia heimii* var. *obtusifolia, Psilopilum cavifolium, Trichostomum cuspidatissimum, Stegonia latifolia,* and *Voitia hyperborea.*

The bryophyte flora of Prince Patrick Island, as revealed by Mr. Handley's

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collection, is surprisingly similar to that of Cornwallis Island (Steere, 1951), in spite of the distance separating them. We find the same preponderance of calciphile species, and an almost complete absence of those elements that require acidic habitats, as *Sphagnum*. Our knowledge of the bryophytes of the two islands is still fragmentary, of course, because the excellent collections from them cannot be either complete or representative, coming as they do from very restricted areas. Nevertheless, it appears that Prince Patrick Island possesses less strongly calcareous habitats, because of the presence there of several species of neutral or slightly acidic habitats apparently lacking on Cornwallis Island.

In the following list of bryophytes, the various species in a mixture are represented by letters following the collection number. To a considerable extent, the relative amount of any species present in the collection is reflected by the position of the letter in the alphabet, "a" representing that species most conspicuous in mixture with the primary species, "b" the next most predominant admixture, etc.

To avoid unnecessary repetition, the name of the collector of all the specimens, Mr. Charles O. Handley, Jr., and the year, 1949, are omitted from the following citations of specimens. Furthermore, where possible, Mould Bay Weather Station, from whose vicinity most of the specimens come, is abbreviated as "MBWS."

PTILIDIACEAE

Blepharostoma trichophyllum (L.) Dumort.—At mouth of Mud River, 7 miles SE. of Mould Bay Weather Station, July 20, 16*l*. This is almost certainly the most common and widely-distributed hepatic in arctic America.

Ptilidium ciliare (L.) Nees.—At mouth of Mud River, 7 miles SE. of Mould Bay Weather Station, July 20, 16*b*. A common and widely-distributed circumpolar hepatic.

CEPHALOZIACEAE

Odontoschisma macounii (Aust.) Underw.—At mouth of Mud River, 7 miles SE. of Mould Bay Weather Station, July 20, 16*m*. Although this hepatic has a broad geographic range, it does not seem to be particularly common within it.

JUNGERMANNIACEAE

Arnellia fennica (Gottsche) Lindb.—On dry, hummocky silt sod on gentle slope, 2 miles NW. of Mould Bay Weather Station, Sept. 3, 61(*a*)*a*. In spite of its rating as a relatively rare species, this hepatic occurs commonly and often in abundance in arctic America.

RICCARDIACEAE

Riccardia pinguis (L.) S. F. Gray.—In perpetual bog 0.5 mile N. of Mould Bay Weather Station, July 11, 14*c*; east side of Manson Point, 9 miles SE. of MBWS., July 21, 18*b*. A very widely distributed hepatic, but rarely occurring in abundance in collections from arctic regions, usually as single individuals.

ANDREAEACEAE

Andreaea rupestris Hedw.—West shore of Mould Bay, 7 miles NNW. of Mould Bay Weather Station, July 7, 7*c*; stony barren on ridge top, 7 miles SE. of MBWS., Aug. 23, 57*c*; head of Straight River, 11 miles NNE. of MBWS., Sept. 1, 60*a*. Previously reported from Devon Island, this species reaches a new northernmost outpost as the result of these collections.

DITRICHACEAE

Ceratodon heterophyllus Kindb.—On relatively dry silt-erosion hummocks, 6.5 miles SE. of Mould Bay Weather Station, Aug. 6, 31*d*. According to Grout (1936), this species has been reported only from St. Paul Island, the type locality, and from Agattu

Island. In addition to the collection cited here, it has been found in some abundance in arctic Alaska, especially at Point Barrow, by the present author in 1951 and 1952. It now seems safe to maintain this as a good species, in spite of its highly variable and weedy relatives, because of its wide distribution, and its constant morphological distinctness.

Ceratodon purpureus (Hedw.) Brid.—In dry river flat, 1.5 miles NE. of Mould Bay Weather Station, Aug. 8, 34*a*; in hillside seep, 2 miles NW. of MBWS., Sept. 3, 62*m*. A variable cosmopolitan weed.

Distichium uapillaceum (Hedw.) BSG.—Disappointment Point, Intrepid Inlet, on mud slopes, June 29, 3*d*; from many localities in vicinity of Mould Bay Weather Station, to a distance of 8.5 miles, June 29 to Sept. 3:   4*d*, 9*c*, 10*a*, 1 ', 13*e*, 14*f*, 15, 19*a*, 20*a*, 21*f*, 23(*b*)*d*, 25, 26*i*, 27*g*, 29*d*, 30*b*, 36*f*, 37*a* 38*c*, 41*e*, 44*d*, 45*i*, 47*b*, 50*f*, 52*a*, 53*a*, 54*g*, 55*o*, 58*b*, 59*f*, 61(*a*)*b*, 62*i*. A weedy species of calcareous habitats, with a very wide distribution in the cooler regions of the world.

Distichium hageni Ryan.—Dry silt-loam with scanty vegetation, near mouth of Mud River, 6 miles SE. of Mould Bay Weather Station, July 20, 17; crest of sandy ridge, barren except along seeps, 2.5 miles ESE. of MBWS., July 27, 23(*a*); sandy riverbank 1.5 miles NE. of MBWS., Aug. 9, 36*b*. These collections greatly extend the American range of a truly arctic species reported previously from the Canadian Eastern Arctic, (Bryhn, 1907), from Newfoundland (Bartram, 1925) and from the east coast of Hudson Bay (Wynne and Steere, 1943). Furthermore, the present author has found this species in several widely separated areas of arctic Alaska during 1951 and 1952, confirming its truly arctic distribution.

Ditrichum flexicaule (Schwaegr.) Hampe.—Disappointment Point, Intrepid Inlet, on mud slopes, June 29, 3*a*; from vicinity of Mould Bay Weather Station, to a distance of several miles, in many types of habitats, June 30 to Sept. 3: 00, 1*d*, 3*a*, 7*f*, 8, 9*b*, 10*c*, 13*d*, 14*b*, 15*i*, 16*f*, 17*a*, 18*c*, 20*h*, 21*e*, 26*b*, 29*e*, 35*c*, 38*i*, 39*d*, 41*a*, 45*c*, 46, 47*a*, 48*a*, 50*g*, 53*h*, 54*t*, 55*b*, 59*t*, 60*c* 61(*a*)*f*, 61*b*, 62*j*, 63. A common and abundant moss in boreal regions, and one that tolerates great variability in moisture and pH.

DICRANACEAE

Dicranum laevidens Williams.—Marshy flat, Crozier Channel 8 miles ESE. of Mould Bay Weather Station, July 31, 28*a*; hummocky, potholed mountain slope above Peak Creek, 8.4 miles ENE. of MBWS., Aug. 14, 42*a*. A species of arctic America which Persson (1952) has very recently considered to be a simple synonym of *D. angustum* Lindb.

Dicranoweisia crispula (Hedw.) Lindb.—West shore of Mould Bay, 7 miles NNW. of Weather Station, July 7, 7*b*; 2.5 miles SE. of MBWS., July 27, 22*f*; stony barren on ridge top, 7 miles SE. of MBWS., Aug. 23, 57*e*; head of Straight River, 11 miles NNE. of MBWS., Sept. 1, 60*d*. The occurrence of this species is of significance in that it usually occurs on non-calcareous rocks or other substrata.

Oncophorus wahlenbergii Brid.—In perpetual bog near Mould Bay Weather Station, July 11, 14*d*; in bog 7 miles SE. of MBWS., at mouth of Mud River, July 20, 16; in hilltop marsh near MBWS., Aug. 3, 29*i*; wet meadow at mouth of Cherie River, 8 miles ENE. of MBWS., Aug. 14, 41*n*; in marsh at sea level near MBWS., Aug. 22, 54*u*; inland marsh, 2 miles NE. of MBWS., Aug. 22, 55*a*. In arctic regions, this is a species of neutral to calcareous marshes.

Oreoweisia serrulata (Funck) De Not.—In mossy marsh in Bent Creek Gorge, 5 miles NNW. of Mould Bay Weather Station, 400 ft. alt., Aug. 16, 48*b*. This seems to be by far the northernmost locality in North America for a relatively rare species.

ENCALYPTACEAE

Bryobrittonia pellucida Williams.—On sandy riverbank, 1.5 miles NE. of Mould Bay Weather Station, Aug. 9, 36*i*; dry, hummocky silt sod on gentle slope above beach, 2 miles NW. of MBWS., Sept. 3, 61(*a*)*j*, 61(*b*)*g*. These collections represent a major extension of geographic range, fully a thousand miles northward from the type locality, for a species whose systematic position has been established certainly only very recently (Steere, 1953). Although proposed more than a half century ago (Williams, 1901) for a single sterile collection from the Yukon Territory, this monotypic genus was not recognized again until a few years ago, when Persson (1946) reported two collections from the Seward Peninsula of Alaska. The present author has collected this interesting moss at Coppermine, NWT.,

Canada, and at several localities on the arctic slope of Alaska, where sporophytes were finally found.

Encalypta procera Bruch.—East shore of Mould Bay, 7 miles NNW. of Mould Bay Weather Station, July 11, 11*a*; on mud seep, 4.5 miles NE. of MBWS., Aug. 14, 44*b*; shale barren, top of Roughleg Mt., 4 miles N. of MBWS., Aug. 16, 47*f*; moist hilltop seep, on old caribou antler, 2 miles N. of MBWS., Aug. 21, 53*f*; dry, hummocky silt sod, gentle slope above beach, 2 miles NW. of MBWS., Sept. 3, 61(*b*)*j*. This species is not uncommon at high latitudes, especially in the Canadian Western Arctic.

Encalypta rhabdocarpa Schwaegr.—East slope of Round Hill, 2 miles SE. of Mould Bay Weather Station, July 25, 20; southern exposure, near MBWS., July 28, 25*f*; dry hummock in wet tundra, 4 miles SE. of MBWS., Aug. 10, 37*c*; in dry tundra about MBWS., Aug. 13, 38*t*; barren sandy crests, 800 ft. alt., 8 miles NE. of MBWS., Aug. 14, 43; on dry hummocky sod, 1.5 miles N. of MBWS., Aug. 16, 45*m*; on dry, hummocky silt sod, 2 miles NW. of MBWS., Sept. 3, 61(*a*)*e*, 61(*b*)*b*. A relatively common and abundant species in arctic regions.

POTTIACEAE

Anoectangium tenuinerve (Limpr.) Paris.—On old caribou antler in moist seep on hilltop, 2 miles N. of Mould Bay Weather Station, Aug. 21, 53*d*; on top of dividing ridge, in moss-tundra, 4-5 miles ESE. of MBWS., Aug. 23, 59*j*; upper margin of coastal hills, 6 miles SE. of MBWS., Aug. 30, 63*c*. Although widely distributed in northern areas, this species appears to be neither common nor abundant.

Barbula icmadophila Schimp.—In many localities in the vicinity of Mould Bay Weather Station, to a distance of several miles, June 28 to Sept. 3: 0*b*, 9*h*, 11*g*, 14*j*, 15*e*, 20*c*, 23(*a*), 30*c*, 36*j*, 37*d*, 38*r*, 39*c*, 44*a*, 45*l*, 50*i*, 51*f*, 53*b*, 54*x*, 59*k*, 61(*a*)*d*. The abundance of this species in the Canadian Western Arctic is surprising indeed, in view of its rarity in the eastern islands (Steere, 1948, 1951). It is also abundant in arctic Alaska.

Bryoerythrophyllum recurvirostre (Hedw.). Chen, Hedwigia 80:5. 1941. (*Didymodon* Jennings; *Erythrophyllum* Loeske, 1908, *non* Agardh, 1871; *Erythrobarbula* Steere, 1951.) In many localities in the vicinity of Mould Bay Weather Station, to a distance of 10 miles, June 28 to Sept. 3: 0*z*, 4*f*, 9, 11*e*, 13*q*, 20*d*, 23(*b*)*i*, 35*d*, 36*g*, 38*s*, 47*h*, 48*j*, 59*p*, 61(*b*)*e*. This species is not uncommon in all boreal regions, on calcareous habitats.

Correction: The author is obliged to call attention, at this earliest opportunity, to his error in a recent contribution to this same series (Steere, 1951), in proposing the new name *Erythrobarbula* to replace *Erythrophyllum* Loeske (a later homonym of *Erythrophyllum* Agardh), and to the necessity for abandoning this superfluous name. Chen (1941) had already effected this required change of names in a war-time volume of Hedwigia which most unfortunately escaped the attention of the writer, who now wishes to acknowledge with gratitude the kindness of several colleagues who brought Chen's paper to his attention.

Desmatodon leucostomus (Brown) Berggren.—On dry, sparsely vegetated hillside near Mould Bay Weather Station, Aug. 5, 30; in dry river flat, 1.5 miles NE. of MBWS., Aug. 8, 34*b*; on dry, hummocky silt sod, 2 miles NW. of MBWS., Sept. 3, 61(*b*)*k*. This species seems to have a very wide distribution in northernmost North America.

Didymodon rufus Lor.—Moss-marsh in Bent Creek Gorge, 5 miles NNW. of Mould Bay Weather Station, Aug. 16, 48*i*; in sea-level marsh near MBWS., Aug. 22, 54*y*. This is a rare species whose distribution in arctic America is still very incompletely known.

Pottia heimii (Hedw.) Fürnr. var. *obtusifolia* (Brown) Hagen.—East shore of Mould Bay, 7 miles NNW. of Weather Station, July 11, 11*c*; sandy riverbank, 1.5 miles NE. of MBWS., Aug. 9, 36; Shale barren, top of Roughleg Mt., 4 miles N. of MBWS., Aug. 16, 47*g*. This typically arctic moss occurs abundantly on calcareous silts, sometimes in very great abundance. The silty sea cliffs at Point Barrow, Alaska, for example, are colored yellow, orange, and red by large patches of this moss in different stages of maturity, toward the end of the summer. After careful field study of this moss in the field, the author believes that it may eventually need to be restored to the status of a species.

Stegonia latifolia (Schwaegr.) Vent.—On east slope of Round Hill, 2 miles SE. of Mould Bay Weather Station, at 40 ft. alt., July 25, 20*g*. The usual habitat of this species, like the preceding, is a fine calcareous silt. Although with a wide distribution in arctic America, few collections appear to have been made.

Tortella tortuosa (Hedw.) Limpr.—In marsh on hilltop near Mould Bay Weather Station, Aug. 3, 29*h*; inland marsh 2 miles NE. of MBWS., Aug. 22, 55. A not uncommon species on calcareous substrata in all boreal regions.

Tortula mucronifolia Schwaegr.—On dry silt, north slope of Round Hill, 1 mile SE. of Mould Bay Weather Station, July 18, 15*d*; in dry river flat, 1.5 miles NE. of MBWS., Aug. 8, 34*d*; on barren sandy crests, 800 ft. alt., 8 miles NE. of MBWS., Aug. 14, 43*c*; top of Roughleg Mt., 100 ft. alt., 4 miles N. of MBWS., Aug. 16, 47*j*; between hummocks of soil on dry ridge near MBWS., Aug. 17, 50*k*; in moist seep on hilltop 2 miles N. of MBWS., Aug. 21, 53*g*. Although apparently common on Prince Patrick Island and on Cornwallis Island, this species has been collected with surprising rarity elsewhere in arctic America (Steere, 1948).

Tortula ruralis (Hedw.) Smith.—On mud slopes, Disappointment Point, Intrepid Inlet, June 29, 3*i*; in many localities in the vicinity of Mould Bay Weather Station, within a radius of 10 miles, June 28 to Aug. 23: 0*e*, 00*b*, 4, 8*a*, 11*b*, 12*a*, 14*i*, 15*b*, 17*f*, 18*d*, 20*f*, 21*g*, 23(*a*)*b*, 23(*b*)*a*, 25*a*, 33, 36*d*, 37*e*, 38*h*, 43*a*, 45*h*, 50*c*, 51*d*, 59*r*. This is a variable and somewhat weedy species of calcareous habitats over much of the world.

Trichostomum cuspidatissimum Card. & Thér.—On mud slopes above beach, Disappointment Point, Intrepid Inlet, June 29, 3*h*. This collection adds greatly to our knowledge of a rare and interesting arctic moss, whose distribution pattern is gradually taking form as more localities for it are discovered. Until a very few years ago this species was known only from the type locality on Hall Island, Alaska.

GRIMMIACEAE

Grimmia gracilis Schleich.—On top of dividing ridge, 700 ft. alt., vicinity of Mould Bay Weather Station, in moss-tundra (soil frozen), Aug. 23, 59*o*. A rather common arctic-montane species of calcareous habitats.

Rhacomitrium canescens Brid.—In tundra, 2.5 miles SE. of Mould Bay Weather Station, July 27, 22*c*; in mucky tundra on old caribou antler, 3 miles SE. of MBWS., Aug. 7, 33*g*; in dry tundra about MBWS., Aug. 13, 38*o*; stony barren on ridge top, 7 miles SE. of MBWS., Aug. 23, 57. This widely-distributed circumpolar species seems, like the next, to have a broad tolerance in the pH of its habitat, tolerating both acidic and calcareous substrata.

Rhacomitrium lanuginosum (Hedw.) Brid.—West shore of Mould Bay, 7 miles NNW. of Weather Station, July 7, 7*a*; in tundra 2.5 miles SE. of MBWS., July 27, 22*b*; 6.5 miles SE. of MBWS., Aug. 6, 31*c*; in dry tundra about MBWS., Aug. 13, 38*w*; on river delta near MBWS., Aug. 17, 49*h*; stony barren on ridge top 7 miles SE. of MBWS., Aug. 23, 57*a*; head of Straight River 11 miles NNE. of MBWS., Sept. 1, 60. This is one of the commonest of arctic mosses; its relative rarity on Prince Patrick Island seems to indicate the prevalence of calcareous areas beyond its tolerance.

Rhacomitrium microcarpon (Hedw.) Lindb.—Cherie Bay, some 10 miles NE. of Mould Bay Weather Station, June 28, 0*f*. This collection establishes the northernmost station for a species much commoner at lower latitudes.

SPLACHNACEAE

Haplodon wormskioldii (Hornem.) R. Br.—West side of Manson Point, 9 miles SE. of Mould Bay Weather Station, July 21, 18*a*; on old muskox dung in marsh, 2.5 miles ESE. of MBWS., July 28, 27; inland marsh, 2 miles NE. of MBWS., Aug. 22, 55*q*. A very widely ranging characteristically arctic species.

Tetraplodon mnioides (Hedw.) BSG.—In flat at mouth of Mud River, 7 miles SE. of Mould Bay Weather Station, July 20, 16*k*; in tundra 2 miles ESE. of MBWS., July 27, 24*a*. A relatively common species of northern regions, on dung, bones, and other highly nitrogenous substrata.

Splachnum vasculosum Hedw.—In sea-level marsh near MBWS., Aug. 22, 54*o*. A widely-distributed circumboreal species which seems to differ from most of its congeners in not requiring dung as its substratum. Its usual habitat appears to be rich soil.

Voitia hyperborea Grev. & Arn.—On muskox dung in dry river flat 1.5 miles NE. of Mould Bay Weather Station, Aug. 8, 35*f*; on muskox dung in moist tundra near MBWS., Aug. 14, 39*h*; in hillside seep 2 miles NW. of MBWS., Sept. 3, 62*n*. Since the type

locality of this species is Melville Island, directly adjacent to the southeast, its occurrence here is not surprising. From a study of a series of specimens of this species, it appears that it reaches its best development on the dung of the muskox, a curious specialization paralleled by other species in this family of nitrophilous mosses.

BRYACEAE

Bryum inclinatum (Web. & Mohr) Sturm.—In several localities in vicinity of Mould Bay Weather Station, within a radius of 4 miles, July 28 to Aug. 21: 25*d*, 30*a*, 31*e*, 34, 37, 38, 53. One of the commonest arctic species of *Bryum*.

Bryum tortifolium Funck (*B. obtusifolium* Lindb.).—West shore of Mould Bay, 7 miles NNW. of Weather Station, July 7, 7*e*; east shore of Mould Bay, 7 miles NNW. of MBWS., July 11, 11*d*; wet meadow at mouth of Cherie River, 8 miles ENE. of MBWS., Aug. 14, 41*o*; inland marsh 2 miles NE. of MBWS., Aug. 22, 55*c*; top of dividing ridge, 4-5 miles ESE. of MBWS., Aug. 23, 59*a*; hillside seep 2 miles NW. of MBWS., Sept. 3, 62*q*. The large, conspicuously red, easily recognized form of this species that Lindberg called *B. obtusifolium* is very widespread in arctic America, occurring in very wet places.

Byrum weigelii Spreng.—In vegetated marsh, 7.5 miles ESE. of Mould Bay Weather Station, Aug. 6, 32. This seems to be the northernmost locality known in North America for a well-characterized species.

Leptobryum pyriforme (Hedw.) Schimp..—Hillside seep 2 miles NW. of Mould Bay Weather Station, Sept. 3, 62*l*. A weedy, cosmopolitan species, more remarkable for its apparent rarity than for its presence.

Pohlia cruda (Hedw.) Lindb.—On mud slopes above beach, Disappointment Point, Intrepid Inlet, June 29, 3*g*; in many localities in vicinity of Mould Bay Weather Station, within a radius of 8.5 miles, July 11 to Sept. 3: 10*f*, 11*f*, 21*h*, 25*b*, 27*a*, 31*a*, 33*d*, 38*x*, 42*k*, 45*a*, 50*j*, 55*s*, 56*c*, 58*a*, 59*q*, 61(*b*)*d*, 62*h*. A species of common occurrence, but rarely in abundance, in arctic America.

Pohlia nutans (Hedw.) Lindb.—On dry, hummocky sod above small stream, 1.5 miles N. of Mould Bay Weather Station, Aug. 16, 45*j*; inland marsh 2 miles NE. of MBWS., Aug. 22, 55*r*. A rather weedy circumboreal species.

MNIACEAE

Cinclidium latifolium Lindb.—Mossy border of pond on river delta, at sea level, near Mould Bay Weather Station, Aug. 17, 49; In sea-level marsh near MBWS., Aug. 22, 54*e*. These collections establish what appears to be the northernmost locality for a beautifully distinct species clearly restricted to the high arctic latitudes. Originally described from Siberia, it has recently been recognized to have a fairly wide distribution in arctic America, through collections made in Baffin Island, the Melville Peninsula, and in arctic Alaska.

Cinclidium stygium Sw.—Wet muskeg, 7 miles NNW. of Mould Bay Weather Station, July 11, 13*m*; in marsh near beach, near MBWS., July 28, 26*j*; marshy pond border, 1.5 miles N. of MBWS., Aug. 16, 46*g*; hillside seep, 2 miles NW. of MBWS., Sept. 3, 62*p*. A widely-distributed boreal species, more common at lower latitudes.

Cinclidium subrotundum Lindb.—Wet meadow at mouth of Cherie River, sea level, 8 miles ENE. of Mould Bay Weather Station, Aug. 14, 41*f*. A truly arctic species not uncommon in northern North America.

Mnium affine Bland.—Well-vegetated marsh, 6.5 miles ESE. of Mould Bay Weather Station, Aug. 6, 32*d*; in dry tundra about MBWS., Aug. 13, 38*q*; mountain slope above Peak Creek, 8.5 miles ENE. of MBWS., Aug. 14, 42*f*; inland marsh, 2 miles NE. of MBWS., Aug. 22, 55*e*; mossy tundra, top of dividing ridge, 4-5 miles ESE. of MBWS., Aug. 23, 59*x*. This is a common boreal species of very wide distribution that may become semi-weedy.

Mnium hymenophylloides Hüben.—In wet muskeg, 7 miles NNW. of Mould Bay Weather Station, at 300 ft. alt., July 11, 13*n*; on old muskox dung in marsh 2.5 miles ESE. of MBWS., July 28, 27*e*; marshy border of pond, 1.5 miles N. of MBWS., Aug. 16, 46*d*. An arctic-montane species of circumboreal distribution, usually in crevices of soil or rock.

Mnium hymenophyllum BSG.—In wet muskeg, 7 miles NNW. of Mould Bay Weather Station, at 300 ft. alt., July 11, 13*c*. This moss has a wide distribution on arctic regions, and may become very abundant in marshy localities.

Mnium orthorhynchum Brid.—In wet muskeg, 7 miles NNW. of Mould Bay Weather Station, July 11, 13*g*; dry silt-loam, 6 miles SE. of MBWS., near mouth of Mud River, July 20, 17*h*; 2.5 miles ESE. of MBWS., July 28, 27*f*; in dry tundra about MBWS., Aug. 13, 38*p*; wet meadow at mouth of Cherie River, at sea level, 8 miles ENE. of MBWS., Aug. 14, 41*j*; dry silt on gentle slope, 2 miles NW. of MBWS., Sept. 3, 61(*a*). This common and widely-distributed circumboreal species appears to be a good indicator for the presence of calcium-ion.

AULACOMNIACEAE

Aulacomnium acuminatum (Lindb. & Arn.) Paris.—Moist tundra 0.5 miles NE. of Mould Bay Weather Station, Aug. 14, 39*e*. This large and handsome moss is restricted to high latitudes. Originally described from Siberia, it is now known from a very few, but widely separated localities in arctic North America. It seems to be especially abundant in arctic Alaska.

Aulacomnium palustre (Web. & Mohr) Schwaegr.—In sea-level marsh 0.5 miles SE. of Mould Bay Weather Station, Aug. 22, 54*a*; inland marsh, 2 miles NE. of MBWS., Aug. 22, 55*g*. A circumboreal species more common southwards.

Aulacomnium turgidum (Wahlenb.) Schwaegr.—On mud slopes above beach, Disappointment Point, Intrepid Inlet, June 29, 3*b*; in numerous localities in vicinity of Mould Bay Weather Station, within a radius of 11 miles, June 30 to Sept. 1: 1, 4*h*, 7*g*, 8*e*, 13*i*, 14*e*, 16*j*, 18, 20*k*, 21*a*, 22, 27*b*, 28, 29*b*, 33*a*, 38*g*, 41*g*, 42*b*, 49*i*, 54, 55*f*, 57*d*, 59*n*, 60*b*. This is one of the commonest mosses in wet places throughout arctic regions at least in acidic to somewhat calcareous habitats.

MEESIACEAE

Meesia triquetra (Hook. & Tayl.) Angstr.—Wet meadow at mouth of Cherie River, 8 miles ENE. of Mould Bay Weather Station, Aug. 14, 41*h*; mossy border of pond on river delta near MBWS., Aug. 17, 49*f*; in sea-level marsh near MBWS., Aug. 22, 54*v*. This beautiful moss seems to tolerate wide ranges of pH; although it seems to prefer acidic to neutral habitats, it is sometimes found on frankly calcareous substrata.

Meesia uliginosa Hedw.—In wet muskeg, 7 miles NNW. of Mould Bay Weather Station, July 11, 13*a*; in sea-level marsh, 0.5 miles SE. of MBWS., Aug. 22, 54*w*; inland marsh, 2 miles NE. of MBWS., Aug. 22, 55*l*. A species of somewhat to very strongly calcareous habitats.

CATOSCOPIACEAE

Catoscopium nigritum Brid.—In sea-level marsh, 0.5 miles SE. of Mould Bay Weather Station, Aug. 22, 54*f*; dry silt sod on gentle slope, 2 miles NW. of MBWS., Sept. 3, 61(*a*)*h*. A species characteristic of calcareous marshes.

BARTRAMIACEAE

Bartramia ithyphylla Brid.—In perpetual bog in flat at mouth of Mud River, 7 miles SE. of Mould Bay Weather Station, July 30, 16*i*; in dry river flat, 1.5 miles NE. of MBWS., Aug. 8, 35*e*. A relatively common arctic-montane species of wide distribution.

Conostomum tetragonum (With.) Lindb.—On dry sod above small stream, 1.5 miles N. of Mould Bay Weather Station, Aug. 16, 45*e*. This species prefers acidic to neutral habitats, and usually occurs where accumulations of snow melt late in the season. It has a very broad circumpolar distribution at higher altitudes.

Philonotis fontana (Hedw.) Brid.—In many localities in vicinity of Mould Bay Weather Station, to a distance of 8.5 miles, July 1 to Sept. 3: 4*g*, 8*d*, 9*e*, 13*b*, 26*c*, 27*c*, 29*j*, 39*f*, 40*b*, 41*i*, 42*e*, 48*f*, 49*d*, 51*b*, 54*i*, 55*d*, 59*l*, 61(*b*)*i*, 62*c*. A common and widely-distributed species of neutral to strongly calcareous marshes.

TIMMIACEAE

Timmia austriaca Hedw.—On mud slopes above beach, at Disappointment Point, Intrepid Inlet, June 29, 3*e*; several localities in vicinity of Mould Bay Weather Station, within a radius of 8.5 miles, June 30 to August 23: 00*c*, 2*b*, 13*f*, 14*h*, 15*h*, 17*e*, 20*j*, 21*c*,

23(a)e, 23(b)c, 25e, 37b, 38j, 42i, 50h, 52, 54q, 59e. A very common species in all far northern areas.

Timmia norvegica Zett.—In perpetual bog, 9 miles SE. of Mould Bay Weather Station, east side of Manson Point, July 21, 19f; dry sod above small stream, 1.5 miles N. of MBWS., Aug. 16, 45d; marshy pond border, 1.5 miles N. of MBWS., Aug. 16, 46a; in moist seep on hilltop, 2 miles N. of MBWS., Aug. 21, 53e; sea-level marsh near MBWS., Aug. 22, 54p; on hillside, 2 miles NW. of MBWS., Sept. 3, 61(b)h, 62k. Although rather rarely reported from arctic America in the past, this species appears to be much more common there than previously recognized.

ORTHOTRICHACEAE

Amphidium lapponicum (Hedw.) Schimp.—In marshy area 2 miles NE. of Mould Bay Weather Station, Aug. 22, 55u. A widely distributed circumboreal species, usually on rock.

Orthotrichum killiasii C. Müll.—In dry tundra about Mould Bay Weather Station, Aug. 13, 38n. An arctic-montane species of broad distribution, usually in calcareous habitats. The arctic American species of *Orthotrichum* are in serious need of careful revision, and the identification reported here is made with some hesitation.

THELIACEAE

Myurella julacea (Schwaegr.) BSG.—From many localities in the vicinity of Mould Bay Weather Station, to a distance of 7 miles, July 7 to Aug. 30: 9a, 10, 13p, 15a, 17b, 27h, 29g, 35a, 38l, 48h, 54r, 59h, 63a. A circumboreal species not uncommon in calcareous habitats.

Myurella tenerrima (Brid.) Lindb.—On mud slopes, Disappointment Point, Intrepid Inlet, June 29, 3f; on bare mud, east shore of Mould Bay, 6 miles NNW. of MBWS., July 11, 10e; in wet muskeg, 7 miles NNW. of MBWS., July 11, 13h; dry river flat, 1.5 miles NE. of MBWS., Aug. 8, 35b; mossy marsh in Bent Creek Gorge, 5 miles NNW. of MBWS., Aug. 16, 48g; top of dividing ridge, 4-5 miles ESE. of MBWS., Aug. 23, 59i. Although slightly less common, this species has much the same distribution as the preceding one, and often occurs with it.

THUIDIACEAE

Abietinella abietina (Hedw.) C. Müll.—Crest of sandy ridge, 2.5 miles ESE. of Mould Bay Weather Station, July 27, 23(a)d, 23(b)f. A circumboreal species, common and sometimes abundant on strongly calcareous substrata.

AMBLYSTEGIACEAE

Amblystegium varium (Hedw.) Lindb.—Between hummocks of soil on dry ridge, 0.5 miles SE. of Mould Bay Weather Station, Aug. 17, 50l. Although this is a very common and widely-distributed species in more temperate regions, it does not seem to have been reported previously from arctic Canada.

Calliergon cordifolium (Hedw.) Kindb.—In well-vegetated marsh, Cherie Bay, 6.5 miles ESE. of Mould Bay Weather Station, Aug. 6, 32a; wet meadows at mouth of Cherie River, 8 miles ENE. of MBWS., Aug. 14, 41. A widely distributed circumboreal species, but not as common in the far north as the following. These collections apparently establish a new northernmost locality for the species in North America.

Calliergon giganteum (Schimp.) Kindb.—In marsh near beach, 0.5 miles SE. of Mould Bay Weather Station, July 28, 26; in small stream beside Cherie River, 7 miles ENE. of MBWS., Aug. 14, 40d; mossy border of pond on river delta, near MBWS., Aug. 17, 49e; Mould Bay and Cherie Bay, Aug. 18, 51c; sea-level marsh, 0.5 miles SE. of MBWS., Aug. 22, 54c; hillside seep, 2 miles NW. of MBWS., Sept. 3, 62b. A rather common circumboreal species.

Calliergon sarmentosum (Wahlenb.) Kindb.—On flat at mouth of Mud River, 7 miles SE. of Mould Bay Weather Station, July 20, 16a; west side of Manson Point, 9 miles SE. of MBWS., July 21, 18j; sea-level marsh, 0.5 mile SE. of MBWS., Aug. 22, 54d; inland marsh, 2 miles NE. of MBWS., Aug. 22, 55j; head of Straight River, 11 miles NNE. of MBWS., 1000 ft. alt., Sept. 1, 60f. A typically arctic-montane species, usually in somewhat calcareous waters.

Calliergon stramineum (Brid.) Kindb.—Mountain slope above Peak Creek, 8.5 miles ENE. of Mould Bay Weather Station, Aug. 14, 42*j*. This circumpolar species is common and widely distributed in most of arctic America, but seems to tolerate less calcium-ion than the preceding.

Calliergon turgescens (Schimp.) Kindb.—Mud seep, 4.5 miles NE. of Mould Bay Weather Station, Aug. 14, 44*f*. A frankly calciphile species of broad arctic-montane distribution.

Campylium stellatum (Hedw.) Lange & C. Jens.—In many localities in vicinity of Mould Bay Weather Station, within radius of 11 miles, July 7 to Sept. 3: 9*d*, 16*g*, 18*h*, 19*d*, 23(*b*), 26*g*, 32*b*, 36*a*, 39*b*, 40*a*, 41*d*, 46*c*, 47, 48*d*, 49*c*, 54*n*, 55*i*, 60*g* 61(*a*)*g*, 62*a*. A very widely distributed circumboreal species of neutral to strongly calcareous habitats.

Cratoneuron filicinum (Hedw.) Roth.—In moist seep, barren promontory, 4 miles NW. of Mould Bay Weather Station, west shore, July 9, 9*f*; sandy riverbank, 1.5 miles NE. of MBWS., Aug. 9, 36*e*; mud seep, 4.5 miles NE. of MBWS., Aug. 14, 44; mossy marsh in Bent Creek Gorge, 5 miles NNW. of MBWS., Aug. 16, 48*e*. A pronounced calciphile of very wide geographic distribution in boreal regions.

Drepanocladus lycopodioides (Brid.) Warnst.—In perpetual bog 0.5 miles N. of Mould Bay Weather Station, July 11, 14*a*; in marsh near beach, 0.5 mile SE. of MBWS., July 28, 26*h*; in mossy marsh in Bent Creek Gorge, 5 miles NNW. of MBWS., Aug. 16, 48*c*; in sea-level marsh 0.5 mile SE. of MBWS., Aug. 22, 54*l*. In spite of its large size, this handsome moss has been reported from very few localities in arctic America. However, from recent collections in northernmost Alaska and elsewhere, this species appears to have a much wider distribution than previously recognized, at least in America, and the present specimens are especially helpful in filling an unknown segment.

Drepanocladus revolvens (C. Müll.) Warnst.—In several localities in the vicinity of Mould Bay Weather Station, to a distance of 9 miles, July 6 to August 22: 5*a*, 16*d*, 18*e*, 26*a*, 29*a*, 40*c*, 41*k*, 49*b*, 54*m*, 55*h*. This is a reasonably common circumboreal species, occurring in neutral to strongly calcareous marshes and bogs.

Drepanocladus uncinatus (Hedw.) Warnst.—From many localities in the immediate and general vicinity of Mould Bay Weather Station, within a radius of 10 miles, June 30 to Aug. 23: 1*b*, 4*b*, 8*c*, 13*o*, 15*f*, 17*d*, 21*b*, 23(*a*)*c*, 23(*b*)*e*, 38*m*, 42, 50*d*, 51*e*, 57*b*, 59*m*. A variable and semi-weedy circumboreal species.

Hygrohypnum polare (Lindb.) Broth.—On rocky slope, west shore of Mould Bay, 7 miles NNW. of Weather Station, 300 ft. alt., July 7, 7*d*. This truly arctic species has been known previously in the Canadian arctic only from Ellesmere Island (Steere, 1948).

BRACHYTHECIACEAE

Brachythecium salebrosum (Web. & Mohr) BSG.—Crest of sandy ridge, 2.5 miles ESE. of Mould Bay Weather Station, July 27, 23(*b*)*h*; in sea-level marsh, 0.5 mile SE. of MBWS., Aug. 22, 54*b*; hillside seep, 2 miles NW. of MBWS., Sept. 3, 62. A common and variable circumpolar species, whose arctic ecotypes are especially perplexing and have received many names.

Cirriphyllum cirrosum (Schwaegr.) Grout.—From many localities in vicinity of Mould Bay Weather Station, within a radius of 9 miles, July 11 to Sept. 3: 13, 16*h*, 18*f*, 21*d*, 29*k*, 34*c*, 36*h*, 38*u*, 41*c*, 49*a*, 50*b*, 55*p*, 59, 62*o*. An arctic-montane species with a broad geographic range in arctic America.

Eurhynchium pulchellum (Hedw.) Jennings.—On mud slopes above beach, Disappointment Point, Intrepid Inlet, June 29, 3*c*; in dry tundra about Mould Bay Weather Station, Aug. 13, 38*y*; Aug. 22, 56*e*; top of dividing ridge, 4-5 miles ESE. of MBWS., Aug. 23, 59*s*. Although little reported from arctic regions, this circumboreal species nevertheless appears to be relatively common and widespread in northernmost America. Some useful comments on the variability of this species, and on the relationship to it of *E. substrigosum* have been made recently by Persson (1952).

Tomenthypnum nitens (Hedw.) Loeske).—From many localities in vicinity of Mould Bay Weather Station, to a distance of 10 miles, June 30 to Sept. 3: 1*c*, 4*a*, 5, 13*j*, 14, 18*b*, 19, 20*e*, 21, 26*f*, 29, 32*c*, 39*g*, 42*g*, 46*e*, 58*s*, 55*k*, 59*w*, 61(*b*)*f*, 62*d*. This is probably the most common, abundant, and widely distributed arctic moss, in terms both of geographic range and of habitat tolerance.

ENTODONTACEAE

Holmgrenia chrysea (Schwaegr.) Lindb.—From many localities in the vicinity of Mould Bay Weather Station, within a radius of 10 miles, June 30 to Sept. 3: 1*e*, 5*b*, 7, 8*b*, 9*g*, 17*g*, 23(*a*)*a*, 23(*b*)*g*, 26*d*, 29*f*, 35, 38*a*, 39*a*, 40, 41*b*, 46*b*, 48, 50, 51*a*, 53*c*, 54*j*, 59*b*, 61(*a*)*i*, 61(*b*)*a*, 62*f*. A beautiful and conspicuous arctic-montane species of circumboreal distribution.

Holmgrenia stricta Lor.—On bare mud, east shore of Mould Bay, 6 miles NNW. of Weather Station, July 11, 10*b*; in dry tundra about MBWS., Aug. 13, 38*b*; mud seep, 4.5 miles NE. of MBWS., Aug. 14, 44*e*; top of Roughleg Mt., in shale barren, 4 miles N. of MBWS., Aug. 16, 47*i*; sea-level marsh 0.5 mile SE. of MBWS., Aug. 22, 54*k*; top of dividing ridge 4-5 miles ESE. of MBWS., Aug. 23, 59*c*; hillside seep, 2 miles NW. of MBWS., Sept. 3, 62*e*; upper margin of coastal hills, 6 miles SE. of MBWS., Aug. 30, 63*b*. These collections add considerably to our knowledge of the geographic distribution of a species that has been reported from a few localities in the Canadian Eastern Arctic (Steere, 1948).

HYPNACEAE

Amblystegiella sprucei (Bruch) Loeske.—Cherie Bay, June 28, 0*g*; top of dividing ridge 4-5 miles ESE. of Mould Bay Weather Station, Aug. 23, 59*v*; on hillside, 2 miles NW. of MBWS., Sept. 3, 61(*a*)*c*, 62*g*. Although rarely abundant, this minute moss has a very wide circumpolar distribution.

Breidleria pratensis (Koch) Loeske.—In wet meadow at mouth of Cherie River, 8 miles ENE. of Mould Bay Weather Station, Aug. 14, 41*m*; shale barren, top of Roughleg Mt., 4 miles N. of MBWS., Aug. 16, 47*d*; mossy border of pond on river delta, near MBWS., Aug. 17, 49*g*. A rare species in arctic Canada, whose range is extended considerably to the north by these collections.

Ctenidium molluscum (Hedw.) Mitt.—Top of dividing ridge, 700 ft. alt., 4-5 miles ESE. of Mould Bay Weather Station, Aug. 23, 59*d*. This seems to be the first report of this circumboreal species from arctic Canada.

Ctenidium procerrimum (Mol.) Lindb.—Between hummocks of soil on dry ridge, 0.5 mile SE. of Mould Bay Weather Station, Aug. 17, 50*e*. This species is known in North America only from a few collections from Ellesmere and Devon islands resulting from the "Fram" Expedition (Bryhn, 1907). The specimen cited here, together with several collections made by the present author in arctic Alaska, give this species a much broader American distribution.

Hypnum bambergeri Schimp.—In marsh on hilltop, 0.5 mile NE. of Mould Bay Weather Station, Aug. 3, 29*l*. This collection appears to represent the northernmost locality known in North America for a handsome circumboreal species.

Hypnum callichroum Brid.—In marshy flat at sea level, Crozier Channel, 8 miles ESE. of Mould Bay Weather Station, July 31, 28*b*. This is not a common species in arctic America, and this specimen seems to represent its northernmost extension, as presently known.

Hypnum cupressiforme Hedw.—Several collections from vicinity of Mould Bay Weather Station, within a radius of 9 miles, July 11 to Aug. 22: 12, 14*g*, 15*j*, 18*i*, 20*i*, 33*f*, 38*e*, 47*c*, 50*a*, 56. Although not uncommon on the northernmost American mainland, this species seems to be rare in the Canadian Arctic Archipelago, and the present specimens establish a new northernmost geographic range in America.

Hypnum revolutum (Mitt.) Lindb.—On mud slopes above beach, Disappointment Point, Intrepid Inlet, June 29, 3; Cherie Bay, June 28, 0*c*, June 30, 00*a*; from many localities in vicinity of Mould Bay Weather Station, within range of 9 miles, June 20 to Aug. 22: 4*e*, 15*g*, 17*c*, 18*c*, 25*c*, 33*b*, 43*b*, 45*f*, 47*e*, 56*a*. A circumpolar species not uncommon in arctic America.

Isopterygium pulchellum (Hedw.) Jaeg.—In perpetual bog on slope, east side of Manson Point, 9 miles SE. of Mould Bay Weather Station, July 21, 19*e*. Since this species appears to be one of the most common and widely distributed in arctic America, although rarely in abundance, its seeming sparsity on Prince Patrick Island is surprising.

HYLOCOMIACEAE

Hylocomium splendens (Hedw.) BSG.—Several localities in vicinity of Mould Bay Weather Station, to a distance of 8.5 miles, June 30 to Aug. 22: 2*a*, 4*c*, 13*k*, 16*c*, 33*e*,

38*k*, 42, 55*m*. It is surprising that so few collections of this species were made, since it is usually the most common and abundant moss in almost every habitat in arctic America.

POLYTRICHACEAE

Pogonatum alpinum (Hedw.) Röhl.—On mud slopes above beach, Disappointment Point, Intrepid Inlet, June 29, 3*j*; from many localities at and near Mould Bay Weather Station, within a radius of 11 miles, June 28 to Sept. 1: 0*d*, 1*a*, 2, 10*g*, 13*l*, 15*c*, 16*e*, 18*g*, 19*g*, 22*a*, 23(*a*)*f*, 24, 26*e*, 27*d*, 29*c*, 31*b*, 33*c*, 38*d*, 41*l*, 42*c*, 45*b*, 46*f*, 53*i*, 54*h*, 55*n*, 56*d*, 57*g*, 59*g*, 60*e*. A common and abundant species of colder circumpolar regions.

Pogonatum capillare (Rich.) Brid.—In stony barren on ridge top, 7 miles SE. of Mould Bay Weather Station, Aug. 23, 57*f*. As this species is little known from arctic America, this specimen is helpful in establishing one segment of its geographic range.

Polytrichum juniperinum Hedw.—In dry tundra about Mould Bay Weather Station, Aug. 13, 38*v*; mountain slope above Peak Creek, 8.5 miles ENE. of MBWS., Aug. 14, 42*h*; inland marsh, 2 miles NE. of MBWS., Aug. 22, 55*t*. Not uncommon in the colder parts of the whole world.

Polytrichum piliferum Hedw.—In and around pothole, 2.5 miles SE. of Mould Bay Weather Station, July 27, 22*e*; on relatively dry silt-erosion hummocks, 6.5 miles SE. of MBWS., Aug. 6, 31*f*; dry hummocky sod above small stream, 1.5 miles N. of MBWS., Aug. 16, 45; top of dividing ridge, moss tundra, 4.5 miles ESE. of MBWS., Aug. 23, 59*u*. This species, which has a nearly worldwide distribution, tolerates little calcium and prefers acidic or sterile substrata.

Psilopilum cavifolium (Wils.) Hagen.—On undercut edge of silt hummock, Cherie Bay, 6 miles NE. of Mould Bay Weather Station, June 30, 2*c*; west shore of Mould Bay, 5.5 miles NW. of Weather Station, July 7, 6; on bare mud, east shore of Mould Bay, 6 miles NNW. of MBWS., July 11, 10*d*; relatively dry silt-erosion hummocks, 6.5 miles SE. of MBWS., Aug. 6, 31; dry, hummocky sod above small stream, 1.5 miles N. of MBWS., Aug. 16, 45*k*; stony barren on ridge top, 7 miles SE. of MBWS., Aug. 23, 57*h*; on beach of Crozier Channel, 8.5 miles SE. of MBWS., Aug. 23, 58. This species, interesting for its restricted distribution in very high latitudes, seems to reach its best development and greatest abundance in the coastal plain of the Arctic Ocean. The present author has found it to be very abundant in the vicinity of Point Barrow and on the north coast of St. Lawrence Island.

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The Ranunculi of the Alaskan Arctic Coastal Plain and the Brooks Range

Lyman Benson

Pomona College, Claremont, California

Until the last five years little has been known of the flora of the Alaskan Arctic Coastal Plain, and the writer has seen only one *Ranunculus* specimen collected in the Brooks Range* prior to 1946. Few of the early collections were made by professional botanists. Nearly all the few specimens are those of members of exploring expeditions not concerned primarily with this field of study, and they record only the existence of species at the few points at which ships stop—nothing of local variability within species. Before 1946 only about twenty collections of *Ranunculus* were known from an area the size of California or of New England, New York, and Pennsylvania. These specimens represent only four species, and they give no indication of geographical distribution because nearly all came from "Point Barrow," Wainwright, or Cape Lisburne.

Since 1946 half a dozen collectors have visited part of the Alaskan Arctic Coastal Plain or the Brooks Range, particularly the United States Navy Petroleum Reserve No. 4 which covers most of the area. Thirteen species of *Ranunculus* are known now to occur on the Coastal Plain and/or in the Brooks Range, according to habitat tolerances. Much of the knowledge of inland distribution of species is derived from the collections of Mr. Lloyd A. Spetzman along the north side of the Brooks Range and of the late Mr. Louis B. Jordal at points on the south side of the same range. Dr. Ira L. Wiggins, Director of the Arctic Research Laboratory at Point Barrow and Director of the Natural History Museum of Stanford University, California, and his assistants Mr. Henry J. Thompson and Mr. John H. Thomas of Stanford University have added materially to the knowledge of distribution of plants in the Point Barrow Region as a result of their extended excursions into the tundra along and away from the immediate coast. Through their kindness, in the summer of 1950 the writer was able to visit various points in the same region and to study more intensively in the field the characters occurring from individual to individual of all the known species of *Ranunculus* occurring in the Point Barrow Region. These studies were continued in the summer of 1952. The chief features of this paper are 1) a summary of the known species and their distribution in far northern Alaska as a result of the collections of others and the field studies of the writer and 2) data bearing on the interrelationships of species and their degree of distinctness from each other resulting from field study in the American and European Arctic by the writer. As a result state-

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* The Brooks Range is the Alaskan extension of the Rocky Mountain System. Because of the westward curve of the mountain system, the Brooks Range runs east and west, north of the Yukon River from the northern part of the boundary between Alaska and the Yukon toward Bering Strait. The central part of the range is north of Fairbanks.

ments of the status of each of several species are possible, and the key characters and the descriptions of some are revised.

Six of the thirteen species of *Ranunculus* occurring in far northern Alaska belong to the section *Epirotes* of the subgenus *Ranunculus*. The study at Point Barrow has provided data for revision of keys and descriptions particularly in this group. The other seven species are mostly solitary representatives of wide-ranging species complexes. In absence of their near relatives it has not been possible to add data upon intergradation with other species, and interest has centered upon their geographical distribution both locally and in relationship to broader occurrence.

From the standpoint of geographical distribution the thirteen species fall into four groups as follows:

(1) Eight are of circumpolar distribution. Six of these were studied by the writer also under field conditions in 1950 in Swedish Lapland from one to two weeks preceding arrival at Point Barrow. Thus it was possible within a few days to study relationships, to look for intergradation among field populations, and to make comparisons at two points 179° of Longitude apart.

(2) *Ranunculus Sabinei* and *R. pedatifidus* var. *affinis* are strictly North American, the former being a high arctic species related to the circumpolar *R. pygmaeus*, and the latter the North American variety of an otherwise circumpolar species the typical variety of which occurs in America only around the Bering Sea.

(3) *Ranunculus gelidus* and *R. glacialis* var. *Chamissonis*. As discussed under the species themselves (and especially under *R. glacialis* var. *Chamissonis*), *R. gelidus* extends on an elongated track from the Altai Mountains in Siberia to the Bering Sea and thence along the Rocky Mountain System (including the Brooks Range) to Colorado. *R. glacialis* var. *Chamissonis* follows part of this track from eastern Siberia to the Bering Sea and as far into America as to the Brooks Range.

(4) *Ranunculus Gmelinii* occurs from Russia to Point Barrow and the Yukon District, occurring both north and south of the Brooks Range; it is rare in northern Minnesota. In the rest of northern North America it is replaced by varieties. It is an aquatic species, its distribution not being governed by the same factors as terrestrial plants and therefore not to be considered with the preceding species.

Ranunculus kamchaticus ranges from the Altai Mountains to the Bering Sea, barely reaching Continental North America at Wales on the east side of the Strait. This exceedingly inconspicuous species may continue on into the Brooks Range, but so far it has not been collected there or in any other part of the Rocky Mountain System.

The circumpolar occurrence of eight species and the existence of three others as well as *R. kamchaticus* on both sides of the Bering Sea raises a question of the time and mode of their disposal. Migration across land has not been possible since at least Pleistocene and perhaps Tertiary or Mesozoic time. Either these species have persisted for a long period on both continents, most of them without material change of character, or else they have some means of dispersal across considerable bodies of water as across the Bering Sea or among the

islands of the Canadian Arctic Archipelago or between these or North America or Greenland and Europe across the North Atlantic. Their survival in northern Alaska during the Pleistocene glaciations was possible because much of Arctic North America including the east side of the Bering Strait, the Alaskan Arctic Coastal Plain, the Brooks Range, and the Canadian Arctic Archipelago was not glaciated, and these areas were a possible refugium north of the great ice sheet. In this area various arctic species of *Ranunculus* and other genera may have survived during Pleistocene times and their occurrence may be older. According to Hultén,* the water level of the oceans was lowered sufficiently by withdrawal of the water bound up in the Pleistocene ice sheets to make not only a broad land connection between continents on the site of the northern Bering Sea but to make an important species refugium there. Unfortunately, herbaceous species, which constitute almost the entire plant population of the Arctic, are not preserved ordinarily as fossils.

REFERENCES AND HERBARIUM SYMBOLS

With the treatment of each species there is a reference to one or two other papers by the writer. These are as follows: *A Treatise on the North American Ranunculi,* Amer. Midl. Nat. 40(1):1-261. 1948; and *Supplement to a Treatise on the North American Ranunculi,* Ibid. 52(2):328-369. 1954. Reference has been given simply to the *Treatise* with a page number or to the *Supplement* with a page number. The symbols representing the herbaria in which specimens are preserved are the same as those listed on pages 5 and 6 of the Treatise or in the Introduction to the Supplement. Those appearing in this paper are as follows:

DS—Dudley Herbarium, Stanford University, Calif.
GH—Gray Herbarium, Harvard University, Cambridge, Mass.
ISC—Herbarium of Iowa State College, Ames
MICH—Herbarium of the University of Michigan, Ann Arbor
MIN—Department of Botany, University of Minnesota, Minneapolis (in the previous list [Treatise] this was cited as UM)
NY—New York Botanical Garden, Bronx Park, New York City
POM—Herbarium of Pomona College, Claremont, Calif.
RM—Rocky Mountain Herbarium, University of Wyoming, Laramie
UC—Herbarium of the University of California, Berkeley
US—U. S. National Herbarium, Washington, D. C.

ACKNOWLEDGEMENTS

* Hultén, Eric (1937) Outline of the History of Arctic and Boreal Biota During the Quaternary Period:33-34.

to the Arctic Contractors and to the many members of the U. S. Armed Forces who helped to make the trip a safe, pleasant, and interesting one and to facilitate obtaining the research data presented here. (See also the acknowledgements in the Supplement to a Treatise on the North American *Ranunculi.*)

<div align="center">KEY TO THE SUBGENERA</div>

1. Sepals 5; achene not constricted
   2. Achenes or utricles not transversely ridged; petals usually glossy, yellow or rarely red, white, or green
      3. Sepals deciduous soon after or during anthesis; fruits not utricular ....Subgenus *Ranunculus*
      3. Sepals persistent in fruit; fruits utricular; pericarp smooth or sometimes with the lateral and distal portions reticulate; sepals thin, marcescent in fruit; petals red or rarely white; leaves compound, dissected into ligulate leaflets or sometimes simple and deeply parted or divided ....Subgenus *Crymodes*
   2. Achenes roughly transversely ridged; petals not glossy, white, the claws sometimes yellow; aquatic ....Subgenus *Batrachium*
1. Sepals 3 or sometimes 4; achene constricted in the middle; rhizomes present
   2. Portion of the achene distal to the constriction not filled with spongy parenchyma; receptacle greatly enlarged in fruit, depressed-globose; petals white, 5 or commonly 7-10; rhizomes and scapes markedly fistulous, 2-6 mm. in diameter; leaf blades entire or 3-lobed or -parted; aquatic or palustrine ......Subgenus *Pallasiantha*
   2. Portion of the achene distal to the constriction occupied by parenchymatous tissue; receptacle not much enlarged in fruit, subglobose; petals yellow, 5-6; rhizomes and scapes wiry, not fistulous, about 2 mm. in diameter; leaf blades 3-parted and often again lobed or parted; terrestrial or subpalustrine, commonly in wet moss ....Subgenus *Coptidium*

Subgenus RANUNCULUS (Gren. & Godr.) A. Gray (Treatise:24)

<div align="center">KEY TO THE SECTIONS</div>

1. Leaves (either the cauline or the basal) or some of them lobed, cleft, parted, or divided
   2. Style and achene beak present, the achene neither corky-keeled nor with corky thickening on the margin of the body; nectary scale ventral to the nectary, covering it, apically truncate or rounded or the margins prolonged, attached to the petal laterally and forming a pocket ....Section *Epirotes*
   2. Style and achene beak practically lacking or, if otherwise, the achene with a corky keel or with corky thickening on the margin of the body; nectary scale either with the gland in a pocket on *its* ventral surface or else the scale forked and prolonged anteriorly on the surface of the petal or surrounding the gland; aquatic or palustrine ....Section *Hecatonia*
1. Leaves (both cauline and basal) entire, dentate, serrulate, or wavy; dorsoventral measurement of the achene not more than twice or thrice the lateral; nectary scale forming a pocket ....Section *Flammula*

Section EPIROTES (Prantl) L. Benson (Treatise:116)

<div align="center">KEY TO THE SPECIES</div>

1. Sepals covered dorsally with dense, conspicuous, long, *reddish-brown* hairs
   2. Receptable glabrous or sometimes with an apical tuft of usually white hairs; basal leaf blades deeply parted and again crenately shallowly lobed or toothed or the middle lobe entire, thin; achene body about 1.5 mm. long ....1. *R. nivalis*
   2. Receptacle brown-hispid, the hairs sometimes sparse but covering the entire receptacle; basal leaf blades or most of those on an individual plant crenately lobed, thick; achene body 1.8-2 mm. long ....2. *R. sulphureus*
1. Sepals not covered dorsally with *reddish-brown* hairs, usually with white hairs

2. Achenes oblong, obovoid, about 1-1.4 mm. long, 0.6-1 mm. dorsoventrally; basal leaf blade basally angular or subcordate, 3-lobed to -parted, the lobes entire or the lateral ones again 2-lobed or rarely with slight additional lobing, the ultimate divisions broad; sepals four-fifths to fully the length of the petals

   3. Petals 1.5-3.5 or rarely 4 mm. long, 1-2 mm. broad; receptacle glabrous; pedicels diffuse, pointing horizontally or in any direction, often curved basally, glabrous to finely tomentose, about 0.5 mm. in diameter, 4-angled, finely but not conspicuously striate; plant delicate ....4. *R. pygmaeus*

   3. Petals 5-8 mm. long, 3-4 mm. broad; receptacle sparsely long-pilose; pedicels stiffly erect, straight, densely long tomentose (the hairs rather coarse), about 1 mm. in diameter, strongly and coarsely 8-striate in age; plant small (the same height as *R. pygmaeus*, i.e., about 1 dm. including the fruiting pedicels) but robust ....5. *R. Sabinei*

2. Achenes discoid-obovoid, 2-2.5 mm. long, about 2 mm. dorsoventrally; basal leaf blade cordate, 3-divided and again cleft to parted and then lobed, the ultimate divisions usually but not always narrow, often linear; sepals half to three-fourths as long as the petals

   3. Petals about 5 mm. long and 4 mm. broad; receptacle glabrous, 2-6 mm. long in fruit; stems exclusive of the pedicels 5 cm. or less in length ....3. *R. gelidus*

   3. Petals 8-10 mm. long, 5-7 mm. broad; receptacle canescent, usually 7-9 mm. long in fruit; stem exclusive of the pedicels normally 8-40 cm. long ....
...................................6. *R. pedatifidus*

1 Ranunculus nivalis L. (Treatise: 121; Suppl.: 350)

Glabrous or sparsely brown-hirsute terrestrial perennials; flowering stems scapose, erect, 4-17 or 30 cm. long, 1-2 mm. in diameter, 1-flowered, glabrous or brown-hirsute; basal leaf blades often reniform, each broader than long, 1-2 cm. long, 1.3-3 cm. broad, 3-lobed or -parted, the middle lobe entire, the lateral lobes again shallowly 2-4-lobed, sometimes crenate, proximally truncate or cordate and distally rounded, glabrous, the petioles 3-10 cm. long, glabrous or brown-hirsute, cauline leaves 2-3, alternate, the bracts 3-5-parted; pedicels 7-12.5 cm. long in fruit, glabrous or brown-pilose; sepals 6-8 mm. long, 3-5 mm. broad, dorsally densely reddish-brown-hipsid, half or three-fifths the length of the petals, promptly deciduous; petals 8-11 mm. long, 7-12 mm. broad; achenes about 40-50 in a cylindroid or ovoid-cylindroid head 7-10 or 17 mm. long and 5-6 or 7 mm. in diameter, each achene 1.5-1.6 mm. long, about 1.2 mm. dorsoventrally, 0.6 mm. laterally, glabrous, the beak slender, 1-2 mm. long, not recurved; receptacle 6-9 mm. long in fruit, glabrous or rarely with a few (usually white) hairs apically.

Circumpolar. Abundant on both the tundra and the foothills of the north side of the Brooks Range up to 3,000 feet altitude; at least scattering in occurrence up to 4,500 feet on the south side of the Brooks Range. The commonest species, coloring many miles of the Arctic Coast.

In the summer of 1950 the writer observed this species in both Alaska and Swedish Lapland at points approximately 179° of Longitude apart. In both areas it is more common and it ranges farther south than *R. sulphureus*, which is rare except farther north. In Lapland *R. nivalis* is common in the mountains at elevations above 1,500 feet, and it is abundant in wet soil among rocks near snow (e.g. base of Låktatjåkko near the source of the Hole Brook, *L. Benson* 14433 (POM); east side of Snoritjåkko, *L. Benson* 14491a (POM)). In the Point Barrow region, the species is abundant on the open tundra as well as in soil exposed by cracking of the tundra and by ice heaving.

At the only point where *R. sulphureus* was found in the Point Barrow Region (Eskimo graveyard 1 mile southwest of the tip of Point Barrow, *Wiggins* 12585 (DS, POM), *L. Benson* 14563 (POM, US), the two collections having been made simultaneously) the writer found no evidence of interspecific intergradation with *R. nivalis* (*L. Benson* 14569 (POM, US)). This was true also on Jebrentjåkko in Swedish Lapland, where *R. nivalis* was abundant with *R. sulphureus* (*L. Benson* 14492). However, a collection from Anaktuvuk Pass in the Brooks Range (*Spetzman* 1890 (MIN)) includes individuals both with and without hairs on the receptacles, with the robust character of *R. sulphureus,* and with basal leaves (not a sufficient number collected) intermediate between the species. Two collections otherwise typical of *R. nivalis* have brown-hairy receptacles (Point Barrow, *Spetzman,* July 30, 1949 417638 (MIN)); Barter Island, *Spetzman* 1215 in 1948 (MIN). Further field studies of intergradation are needed. These will require examination of character combinations in many individuals.

Specimens collected early in the flowering season of 1952 (*L. Benson* 14913, 14918, 14929, 14933, and 14936 included large numbers of individuals. These revealed no introgression of the characters of *R. sulphureus.*

Specimens examined.—ARCTIC COAST. Cape Lisburne, *Mason* in 1931 (UC); Wainwright, *Andrews* in 1924 (DS); Cape Smyth, 71° 16′ N 156° 40′ W, *White* in 1894 (US); "Point Barrow," *Oldmixon* in 1882 (GH), in 1883 (US), *Seale* in 1896 (DS), *McIlhenny* in 1898 (NY) (several sheets); Pt. Barrow Airbase, *Black* 47F in 1947 (US); Ooglamie-Pt. Barrow, *Murdock* in 1883 (GH); 1 mile inland from Will Rogers Monument 15 miles southwest of Barrow Base, *Wiggins* 12466 (DS, POM); 2½ miles south southwest of Barrow Base, *L. Benson* 14527 (POM, US), and 2 sheets undistributed; 1 mile southwest of Barrow Base, *L. Benson* 14919 (POM, US), 14929 (POM, US); Barrow Base, *Wiggins* 12417 (DS, POM), *J. H. Thomas* 2003 (DS, POM), *H. J. Thompson* 1162 (DS, POM), *L. Benson* 14517 (POM, US), and 1 sheet undistributed, 14557, (POM, US); ½ mile east of Barrow Base, *L. Benson* 14918 (POM, US); 2 miles south of Barrow Base, *H. J. Thompson* 1165 (DS, POM); *L. Benson* 14913 (POM, US); 3½ to 4 miles south of Barrow Base, *J. H. Thomas* 2006 (DS, POM), 2023 (DS, POM), *L. Benson* 14577 (POM, US), and 2 sheets undistributed; 5¾ miles south of Barrow Base, *L. Benson* 14584 (fruits with anthocyan pigmentation) (POM, US), 14585 (fruits green) (POM, US); Lake Ikrowik, *L. Benson* 14936 (POM, US); Barrow 3, 13 miles south of Barrow Base, *Wiggins* 12407 (DS, POM); old beach line 2½ miles southeast of Barrow Base, *L. Benson* 14933 (POM, US); Eskimo cemetery 1 mile southwest of the tip of Pt. Barrow, *L. Benson* 14569 (POM, US), and 2 sheets undistributed; 1.5 miles southeast of Barrow Base, *J. H. Thomas* 2013 (DS, POM); Iko Bay, 18 miles southeast of Barrow Base, *H. J. Thompson* 1152 (DS, POM), 1372 (DS, POM), 1373 (DS, POM), 1397 (DS, POM).

BROOKS RANGE (NORTH SIDE). 1 mile west of Lake Noluk, 68° 47′ N 160° W, *Spetzman* 4261 (MIN); Nuka River, 68° 45′ N 159° 45′ W, *Spetzman* 3589 (MIN); Kakavik Lake, 68° 47′ N 157° 5′ W, *Spetzman* 3844 (MIN); Maybe Creek, 69° 20′ N 154° 30′ W, *Spetzman* 2572 (MIN); Anaktuvuk Pass, 68° 17′ N 151° 25′ W, *Spetzman* 1563 (MIN), 1738 (MIN), 1824 (MIN); Kanayut Lake, 68° 20′ N, 151° W, *Spetzman* 2007 (MIN); Sagavanirktok River, 30 miles from the Arctic Ocean, 69° 53′ N 148° 45′ W, *Spetzman* 152 in 1946 (MIN); Shaviovik River, E. Fork, 69° 28′ N 146° 35′ W, *Spetzman* 226 in 1947 (MIN).

BROOKS RANGE (SOUTH SIDE). Northeast of Nolan, 67° 35′ N 150° 35′ W, *Jordal* 2363 (MICH); 3 miles southeast of Wiseman, 67° 25′ N 150° 25′ W, *Jordal* 2171 (MICH).

RANUNCULUS SULPHUREUS SOLANDER (Treatise: 172; Suppl: 350)

Practically glabrous terrestrial perennials; flowering stems scapose, erect, 3-15 or rarely 24 cm. long, 1.5-4 mm. in diameter, 1-3-flowered, glabrous or

sometimes the pedicels brown-hirsute; basal leaf blades broadly ovate or usually broader than long, 1.5-2.5 cm. long, 1.5-2.5 cm. broad, crenately 5-9-lobed or rarely 3-divided, the middle lobe largest, sometimes again 3-lobed, the blades proximally cuneate to truncate and distally rounded, glabrous or sparingly ciliate at the bases, cauline leaves 1-3, alternate, the bracts 3-parted or -divided; pedicels 4-7 cm. long in fruit, sparsely brown-pilose; sepals 6-8 mm. long, 3-5 mm. broad, dorsally densely and conspicuously brown-hispid, about two-thirds the length of the petals, persistent until young fruits are formed; petals 8-12 mm. long, 6-10 mm. broad; achenes 50-90 in an ovoid-cylindroid or ovoid head 6-7 or 9 mm. long and 5-6 mm. in diameter, each achene flattened-obovoid, 1.8-2 mm. long, about 1.4-1.6 mm. dorsoventrally, 0.6-1 mm. laterally, usually glabrous or rarely sparsely brown-hispid, the beak slender, about 0.9-1 mm. long, straight; receptacle about 5 mm. long in fruit, brown-pilose.

Circumpolar. Rare or uncommon along the Arctic Coast; occasional up to 3,000 feet elevation in the Brooks Range; a plant generally of higher latitudes than *R. nivalis*.

This species grows in the soil among loose rocks in the rills below snow banks at the only point of its known occurrence in Swedish Lapland (north base of Jebrentjåkko, *L. Benson* 14492 (POM)). There the plants are intermingled with *R. nivalis*, but no plants with recombinations of characters were observed. *R. sulphureus* did not form dense tufts. At Point Barrow, Alaska, *R. sulphureus* was found on tundra only 1 to 3 inches thick barely formed on loose gravel just west of the Eskimo graveyard 1 mile southwest of the tip of the point. Here the species occurred sparsely in dense tufts a few inches in diameter. Some of these were composed either of many individuals or of many caudices of the same individual produced in the usual manner for perennial *Ranunculi*, i.e. by offshoots. There were some solitary individuals, but evidently the species is not spreading but mostly persisting under relatively unfavorable conditions. As pointed out under *R. nivalis* (*L. Benson* 14569) there was no indication of intergradation with that species. The same was true for *R. pyg-maeus* (*L. Benson* 14568), which is abundant farther out on the Point.

Specimens examined.—ARCTIC COAST. Eskimo graveyard 1 mile southwest of the tip of Point Barrow (two collections made simultaneously), *Wiggins* 12585 (DS, POM), *L. Benson* 14563 (POM, US), and 4 sheets to be distributed; and *L. Benson* 14937 (POM, US); Iko Bay, 18 miles southeast of Barrow Base, *H. J. Thompson* 1398 (DS, POM); Alaktak, Half-Moon 3, 70° 45′ N 155° W, *Spetzman* 2522 (MIN).

BROOKS RANGE (NORTH SIDE). Nuka River, 68° 47′ N 159° 50′ W, *Spetzman* 4070 (MIN); Oolamnagavik, 68° 45′ N 154° 30′ W, *Chapman* 60 in 1946 (US); Sadlerochit River, 69° 25′ N 145° 10′ W, *Spetzman* 872 in 1948 (MIN); Lake Peters, 69° 30′ N 145° W, *Spetzman* in 1948 (MIN) (in part); Lake Schrader, 69° 25′ N 145° W, *Spetzman* 575 in 1948 (MIN).

3 RANUNCULUS GELIDUS Kar. & Kir. (Treatise: 132; Suppl. : 352)

Nearly glabrous terrestrial perennials; flowering stems about 5 cm. long, 1 mm. in diameter, about 2-3-flowered, glabrous; basal leaf blades simple, broadly cordate or reniform in outline, 5-7 or commonly 20-25 mm. long, 8-11 or commonly 23-34 mm. broad, 3-parted or divided and again cleft and then lobed, the ultimate segments proportionately broad, the sides curved, not parallel, proximally cordate and distally with the lobes rather blunt, glabrous or densely ciliate, cauline leaves alternate, 2.5-5 cm. long in fruit, curly-pubescent

or glabrous; sepals 2.5-5 mm. long, 2.5 mm. broad, white-pilose dorsally, half
to three-fourths the length of the petals, promptly deciduous; petals obovate,
about 5 mm. long, 4 mm. broad; achenes 50-80 in a cylindroid to ovoid-cylindroid head 5-9 mm. long and about 5 mm. in diameter, each achene discoid-obovoid, about 2.5 mm. long, 2 mm. dorsoventrally, 0.7-0.9 mm. laterally,
glabrous, the beak rather stout basally, 0.6-0.7 mm. long, recurved; receptacle
3-8 mm. long in fruit, glabrous or pubescent.

Rare; restricted to arctic regions and high mountain peaks from the Altai
Range in Siberia to the Richardson Mountains near the mouth of the Mackenzie River and southward in the Rocky Mountains as far as central Colorado;
remarkable for a long range with disjunct distribution. Alaska in the Shumigan Islands (Popof), in the Alaska Range, (according to Hultén), and in and
along the north side of the Brooks Range at 1,000 to 2,500 feet elevation.

The collections of Spetzman and the single one by Chapman do much to
add to knowledge of distribution of this rare species, reinforcing the theory
that, although the distribution is partly disjunct, it is not as markedly so as it
would seem from the few known collections (cf. discussion of distribution in
the introduction and under *R. glacialis* var. *Chamissonis*).

Specimens examined.—BROOKS RANGE (NORTH SIDE). Upper Colville River, 68°
47′ N 160° 7′ W, *Spetzman* 3664 (MIN); disturbed ground around squirrel holes, Nuka
River, 68° 45′ N 159° 45′ W, *Spetzman* 3603 (MIN) (mixed with *R. pedatifidus* var.
affinis); Oolamnagavik River north of the Brooks Range, *Chapman* 59 in 1946 (US);
Shaviovik River, 69° 27′ N 146° 34′ W, *Spetzman* 224 in 1947 (MIN).

4 RANUNCULUS PYGMAEUS Wahl. (Treatise: 134; Suppl. : 352)

Glabrous terrestrial perennials; stems scapose, erect or ascending, 1-3 cm.
long, 0.5-1.3 mm. in diameter, 1- or 2-flowered; basal leaf blades simple or ternately compound, semicircular, 5-9 mm. long, 6-11 mm. broad, 3-parted or
-divided, the middle lobe entire or 3-lobed, the two lateral divisions 2-3-lobed
or 2-4-lobed or -cleft, proximally truncate or nearly cordate and distally
rounded in outline; cauline leaves alternate or practically opposite, the bracts
divided, sessile; pedicels up to 12.5 cm. long in fruit, glabrous to densely pubescent; sepals 2-3.6 mm. long, 1.2-2 mm. broad, apically sparsely white-hairy,
the length of the petals, promptly deciduous; petals 1.5-3.5 or 4 mm. long,
1-2.8 mm. broad; achenes 40-50 in an ovoid, subglobose, or cylindroid head
2.5-4 or 7.5 mm. long and 2.5-3 or 4.5 mm. in diameter, each achene obovoid,
about 1 mm. long, 0.8 mm. dorsoventrally, 0.5-0.6 mm. laterally, smooth,
glabrous, the beak slender, 0.3-0.7 mm. long, not recurved; receptacle 1.5-4
mm. long in fruit, glabrous.

Common and abundant in arctic regions around the world; less conspicuous
than *R. nivalis* and therefore less frequently collected. Occurring at from sea
level to 3,000 feet on the north side of the Brooks Range and 4,500 feet on the
south side.

In Swedish Lapland this species grew among rocks by snow banks rimming
cirques (e.g. Lake above the source of the Hole Brook, base of Låktatjåkko,
L. Benson 14440 (POM)). In the Point Barrow Region it is abundant on
the tundra and especially in cracks or areas heaved by ice where the soil is
exposed.

This species was not found to show any evidence of intergradation with

any of its relatives (*R. nivalis, R. sulphureus,* or *R. Sabinei*), and it is clearly distinct from all of them. It is most nearly related to *R. Sabinei,* but at Point Barrow the writer found no evidence of intergradation with that species (cf. *R. Sabinei*).

Specimens examined.—ARCTIC COAST. 1 mile inland from Will Rogers Monument, 15 miles southwest of Barrow Base, *Wiggins* 12469 (DS, POM); 4 miles southwest of Barrow Base, *J. H. Thomas* 2007 (DS, POM); U.S.G.S. Magnetic Observatory, 2 miles southwest of Barrow Base, *J. H. Thomas* 2030 (DS, POM); "Point Barrow," *Oldmixon* in 1882 (GH), in 1883 (US), *McIlhenny* 40 in 1898 (NY); Barrow Airbase, *Black* 20F in 1947 (US); Pt. Barrow, 71° 20′ N 156° 40′ W, *Spetzman* 1507 (MIN), 1523 (MIN), 2389 (MIN); Ooglamie-Pt. Barrow (label apparently as Ooglaamie-Pt. Barrow), *Murdock* in 1883 (GH); Barrow Base, *H. J. Thompson* 1143 (DS, POM), 1158, (DS, POM), 1207 (DS, POM), *L. Benson* 14519, (POM, US), *L. Benson* 14555 (POM, US), and 2 sheets undistributed, 14904 (POM, US), 14942 (POM, US); 2 to 3½ miles southwest of Barrow Base, *H. J. Thompson* 1164 (DS, POM), *Wiggins* 12414 (DS, POM), *L. Benson* 14538 (POM, US); 1 mile southwest of Barrow Base, *L. Benson* 14930 (POM, US), 14931 (POM, US); 1 mile south of Barrow Base, *L. Benson* 14555 (POM, US); 5½ miles south of Barrow Base, *J. H. Thomas* 2018 (DS, POM); Nuwuk, tip of Pt. Barrow, *Wiggins* 12534 (DS, POM), 12568 (DS, POM), *H. J. Thompson* 1187 (DS, POM), *L. Benson* 14909 (POM, US); Eskimo cemetery 1 mile southwest of the tip of Point Barrow, *L. Benson* 14568 (POM, US); 2½ miles east of Barrow Base, *H. J. Thompson* 1154 (DS, POM), Iko Bay, 18 miles southeast of Pt. Barrow, *H. J. Thompson* 1374 (DS, POM).

BROOKS RANGE (NORTH SIDE). Upper Colville River, 68° 47′ N 160° 7′ W, *Spetzman* 3710 (MIN); 1 mile west of Lake Noluk 68° 47′ N 160° W, *Spetzman* 4248 (MIN); Sadlerochit River, 69° 30′ N 145° W, *Spetzman* 1050 (MIN); Sadlerochit River, 69° 25′ N 145° 10′ W, *Spetzman* 1287 (MIN); Lake Schrader, 69° 25′ N 145° W, *Spetzman* 1288 (MIN).

BROOKS RANGE (SOUTH SIDE). Emma Dome, 3 miles south of Wiseman, *Jordal* 2404 (MICH).

5 RANUNCULUS SABINEI R. Br. (Treatise:136)

Nearly glabrous terrestrial perennials; stems erect, 6-12 cm. long, 1-2.5 mm. in diameter, simple or branching, 1-6-flowered, glabrous or sparsely long-pilose; basal leaf blades simple, cuneate in outline, 1-3 cm. long, 1-3.4 cm. broad, *3-lobed or the 2 lateral lobes again 2-lobed or rarely with additional* slight lobing, proximally cuneate and the lobes distally rather obtuse, glabrous or sparsely pilose, the petioles 2.5-5 cm. long, glabrous or sparsely pilose, cauline leaves alternate, consisting of about 3 nearly linear divisions, sessile; pedicels 2-4 cm. long in fruit, densely pilose; sepals 4-7 mm. long, 2-3 mm. broad, markedly white-pilose dorsally, four-fifths to fully the length of the petals, tardily deciduous; petals obovate to nearly oblong, 5-8 mm. long, 3-4 mm. broad; achenes about 50-80 in a cylindroid head 6-10 mm. long and about 4 mm. in diameter, each achene oblong-obovoid, 1.2-1.4 mm. long, 1 mm. laterally, 0.6-0.7 mm. dorsoventrally, smooth, glabrous, the beaks slender, 0.4-0.5 mm. long, straight or the tips bent; receptacle cylindroid, 5-8 mm. long in fruit, sparsely long-pilose.

Point Barrow Region to Greenland; an extreme arctic species known previously from nowhere west of Cape Bathurst, District of Mackenzie, Canada.

The 1950 collections of Thomas and of the writer make possible an accurate description of the fruit of this species.

In the Point Barrow Region *R. Sabinei* occurs on soil exposed by heaving of ice in the tundra, on sandy areas back of the ocean where the beach makes

contact with the tundra, and along tiny ephemeral watercourses on low bluffs above the Arctic Ocean. The species has been found only on the coastal margin of the tundra.

The writer (Treatise:136-7) has discussed the relationship of *R. Sabinei* and *R. pygmaeus* as follows:

"Hultén, Fl. Alaska & Yukon, Lunds Univ. Arrsk. II. 40(1):766. 1944, contends that *R. Sabinei* is a variety of *R. pygmaeus*, as follows: 'In the above material specimens from Pt. Barrow and Ooglamie differ in being very large-grown and robust. They must be said to belong to var. *Sabinei* (R. BR.) KURTZ, characterized by larger size, thick, long peduncles [pedicels] and large flowers with very hairy sepals and constituting an extreme arctic race of *R. pygmaeus*. They are intermediate between the most extreme Var. *Sabinei* and typical *R. pygmaeus*. The specimens from Pt. Barrow, however, do not so definitely belong to that type. The specimens from King I. are also high-grown but represent a form still closer to typical *R. pygmaeus*.' The writer has not seen intermediate plants. Varietal status is not indicated by the results of this study."

The distinctness of this species was studied closely at Point Barrow in August, 1950, and July, 1952, as were specimens collected earlier in the 1950 season by Dr. Ira L. Wiggins and his co-workers Mr. Henry J. Thompson and Mr. John H. Thomas. Although *R. Sabinei* grows with *R. nivalis*, there is no sign of intergradation. This point was checked in the field with particular care on beach sand being invaded by tundra one mile southwest of Barrow Base on July 2, 1952. *R. Sabinei* (*L. Benson* 14932) and *R. pygmaeus* (*L. Benson* 14931) were intermingled, but there was no evidence of character recombination in any individual and no plants were intermediate in character. Although *R. Sabinei* is related closely to *R. pygmaeus*, at Point Barrow neither field nor herbarium studies have shown any intergradation in the several areas where the two species grow together. The reference to collections from Point Barrow by Hultén were based upon robust individuals of *R. pygmaeus* and not *R. Sabinei*. They are cited under *R. pygmaeus* (Pt. Barrow, *Oldmixon* in 1882 (GH); Ooglamie, *Murdock* in 1883 (GH), the two collections being mounted on the same sheet). The only collections of *R. Sabinei* at Pt. Barrow prior to 1950 are by Black in 1947 and by Spetzman (2390 in part), as cited below.

Specimens examined.—ARCTIC COAST. Mouth of estuary 7 miles southwest of Barrow Base, *Wiggins* 12442 (DS, POM), *L. Benson* 14594 (POM, US), and 4 sheets undistributed; Eskimo Village, southwest of Point Barrow, *Spetzman* 2390 (MIN) (in part); 2½ miles south southwest of Barrow Base, *L. Benson* 14546 (US, POM); 1 mile southwest of Barrow Base, *Thomas* 2165 (DS, POM), *L. Benson* 14932 (POM, US); tundra ¼ mile east of Barrow Base, *L. Benson* 14518 (POM, US); Barrow Airbase, *Black 6Fa* in 1947 (US), *6Fb* in 1947 (US). A single individual was observed at the Eskimo graveyard 1 mile south of the tip of Pt. Barrow, *L. Benson* in 1952.

6 RANUNCULUS PEDATIFIDUS J. E. Smith var. AFFINIS (R. Br.) L. Benson
(Treatise: 152, Suppl.: 355)

At least sparingly pilose terrestrial perennials; roots about 0.6-1 mm. in diameter; stems erect, 2-4 dm. long, 2-3 or 4 mm. in diameter, with 1-5 or 8 flowers, pilose to nearly glabrous, striate; basal leaf blades simple, cordate to cordate-orbicular in outline, 1.5-3.5 cm. long, 1.5-4 cm. broad, pedately divided or parted into 5-7 linear divisions some of which are again lobed, the blade proximally cordate, the lobes distally acute or obtuse, thinly pilose to glabrous, the petioles 4-10 cm. long, pilose; cauline leaves alternate, the bracts divided

into 3-7 linear lobes, sessile; pedicels 5-14 cm. long in fruit, pilose, often dense-
ly so; sepals 4-6 mm. long, 3-5 mm. broad, densely white-pilose dorsally, about
half the length of the petals, tardily deciduous after anthesis; petals 8-10 mm.
long, 5-7 mm. broad; achenes 25 or usually 40-70 in a cylindroid head 8-10
mm. long and 5-6 mm. in diameter, each achene flattened-obovoid, 2 mm. long,
1.5 mm. dorsoventrally, 0.6-0.8 mm. laterally, smooth, very finely canescent or
glabrate, the beak slender, 0.6-1 mm. long, recurved; receptacle ovoid, obovoid,
or cylindroid, 7-9 mm. long in fruit, canescent.

Alaska to the Canadian Arctic Islands, Labrador, Newfoundland, and
Greenland and southward to the Rocky Mountain System as far as Arizona
and Colorado and to Saskatchewan. Alaktak, 50 feet elevation near the Arctic
Coast, and in the Brooks Range, mostly at 2,000 to 4,000 feet.

Although this variety has been expected to occur across northern Alaska,
evidence was lacking until numerous collections were made by Spetzman.

Specimens examined.—ARCTIC COASTAL PLAIN. Alaktak, Half-Moon 3, 70° 45' N
155° W, *Spetzman* 2468 (MIN).

BROOKS RANGE (NORTH SIDE). Colville River, 68° 47' N 160° 7' W, *Spetzman*
3718 (MIN); Lake Noluk, 68° 47' N 160° W, *Spetzman* 3503 (MIN), 4008 (MIN);
Nuka River, 68° 45' N 159° 45' W, *Spetzman* 3603 (MIN) (in part); Tuliguk Lake,
Anaktuvuk, *Spetzman* 1843 (MIN); Sagavanirktok River, West Fork, *Spetzman* 7 in
1946 (MIN); Shaviovik River, East Fork, 69° 45' N 146° 57' W, *Spetzman* 296 in
1947 (MIN); Sadlerochit River, 69° 25' N 145° 10' W, *Spetzman* 886 (MIN), 1031
(MIN); Lake Schrader, 69° 25' N 145° W, *Spetzman* 560 (MIN).

Section FLAMMULA (Webb) RUOY & FOUCAUD (Treatise: 170; Suppl.:359)

7 RANUNCULUS FLAMMULA L. var. FILIFORMIS (Michx.) DC.

Circumpolar. Occurring both in forests and beyond timberline in arctic
regions. Umiat, 400 feet, Colville River just north of the Brooks Range; south
side of the Brooks Range.

This plant is called often *R. reptans* L. Differentiation of the extreme ends
of the series in *R. Flammula* seems obvious to those whose concern is with
local floras. However, in North America and Eurasia intergradation of the
three varieties within the species is complete, and specific segregation is unwar-
ranted. Segregation of the two striking forms as species is an excellent example
of failure to consider the whole series instead of the local extremes.

Cf. discussion of distribution under *R. aquatilis* var. *capillaceus.*

Specimens examined.—FOOTHILLS OF THE BROOKS RANGE (NORTH SIDE). Umiat,
69° 30' N 152° W, *Spetzman* 2628 (MIN), *Thompson* 1235a (DS, POM).

BROOKS RANGE (SOUTH SIDE). North of Walker Lake, *Jordal* 4016 (MICH); 50
miles north of Bettles, *Jordal* 2464 (MICH); Old John Lake, *Jordal* 3936 (MICH);
Arctic Village, *Jordal* 3606 (MICH).

Sect. HECATONIA (Lour.) DC. (Treatise:200)

KEY TO THE SPECIES

1. Styles and achene beaks practically lacking, the stigmas nearly sessile; achene with-
   out marked thickening of the pericarp; leaves not cordate at the bases, not dis-
   sected, 3-lobed, the lobes entire or notched; receptacle glabrous in fruit ....
   ....8. *R. hyperboreus*

1. Styles and achene beaks well-developed, the beaks at least half as long as the achene
   bodies; achene with corky thickening on the sides toward the base; leaves cordate

basally, 3-parted or -divided and again 3-lobed to -parted, usually finely dissected
into linear, acute divisions; receptacle hairy ....9. *R. Gmelinii*

8 RANUNCULUS HYPERBOREUS Rottb. (Treatise:201)

Circumpolar and in several of the higher mountain ranges of the northern
portions of the Northern Hemisphere. Point Barrow Region and possibly but
not certainly all along the Arctic Coast; near Lake Noluk in the Brooks Range
at about 2,200 feet elevation.

This species occurs in pools and puddles and on the mud at their margins.
In July, 1950, it was observed in Swedish Lapland growing in water of a rill
(along the railroad 1 mile east of Abisko Östra, south side of Lake Torne-
träsk, *L. Benson* 14368 (POM)). In August, 1950, it was observed near
Point Barrow in pools on the tundra and in mud on their margins (1 mile
south of Barrow Base, *L. Benson* 14561).

The plants (Treatise:201) referred by Hultén to subsp. *samojedorum*
(Rupr.) Hult. have been examined at Stockholm. The writer (in view of
very conservative policy) prefers to consider this plant as a minor taxon to be
mentioned but not named. The leaves are parted deeply, the lobes tending
towards narrowly oblong or linear; the sinuses are therefore broad. This
character is approached in larger plants cited by Hultén, e.g. Healy, Alaska,
J. P. Anderson 5712 (S) (except the plant at the upper left). Some leaves
of plants collected near Point Barrow, Alaska, approach those cited as var.
samojedorum (cf. *L. Benson* 14561 and *H. J. Thompson* 1401 listed below).

Specimens examined.—ARCTIC COAST. 1 mile southwest of Barrow Base, *J. H. Thom-*
as 2163 (DS, POM); 1 mile south of Barrow Base, *L. Benson* 14561 (POM, US); Iko
Bay, 18 miles southeast of Barrow Base, *H. J. Thompson* 1401 (DS, POM).

BROOKS RANGE (NORTH SIDE). Lake Noluk, 68° 47′ N 160 ° W, *Spetzman* 4293
(MIN), *H. J. Thompson* 1308 (DS, POM).

9 RANUNCULUS GMELINII DC. var. GMELINII (Treatise:206;
Suppl. : 362)

Northern European Russia; Siberia; northern Mongolia; northern Alaska
to Keewatin and Peace River, Alberta; rare in northern Minnesota. Arctic
Coast and both the north and south sides of the Brooks Range.

This plant was observed submerged and fruiting, clearly having flowered
under water (Alaska. Pools in tundra roughened and elevated several feet
by ice heaving, 13 miles south of Barrow Base, 71° 9′ N, 156° 34′ W, *L.
Benson* 14591 (US, POM)).

Specimens examined.—ARCTIC COAST. Wainwright, *J. P. Anderson* 4366 (ISC);
estuary near Will Rogers Monument, 15 miles southwest of Barrow Base, *Wiggins* 12501
(DS, POM); Ooglamie, Pt. Barrow, *Murdock* in 1883 (GH); "Point Barrow," *Murdock*
in 1883 (GH, US); A'aktak, Half-Moon 3, 70° 45′ N 155° W, *Spetzman* 2469
(MIN); 13 miles south of Barrow Base, 71° 9′ N, 156° 34′ W, *L. Benson* 14591
(POM, US), and 4 sheets to be distributed; Iko Bay, 18 miles southeast of Barrow
Base, *J. H. Thomas* 2184 (DS, POM), *H. J. Thompson* 1400 (DS, POM).

BROOKS RANGE (NORTH SIDE). 1 mile west of Lake Noluk, 68° 47′ N 160° W,
Spetzman 4253 (MIN); Lake Noluk, *Spetzman* 3919 (MIN), 4297 (MIN), *H. J.
Thompson* 1307 (DS, POM); Seabee Creek, 69° 30′ N 125° W, *Spetzman* 3919
(MIN); Umiat, *H. J. Thompson* 1235 (DS, POM); Sagavanirktok River, West Fork
10 miles above junction, 69° 30′ N 147° 50′ W, *Spetzman* 103 in 1946 ((MIN); Sad-
lerochit River, 69° 35′ N 144° 45′ W, *Spetzman* 1101 (MIN).

BROOKS RANGE (SOUTH SIDE). Wiseman, *Scamman* 2254 (GH), *Jordal* 2193 (MICH).

Subgenus CRYMODES A. Gray (Treatise:224)

10   RANUNCULUS GLACIALIS L. var. CHAMISSONIS (Schlecht.) L. Benson
(Treatise: 226; Suppl. : 364)

Eastern Siberia and Alaska. Thunder Mountain, western portion of the Brooks Range; 4,000 feet.

The single collection by Spetzman extends the known range of this plant about 200 miles northeastward from its only previously established occurrence in continental North America near Wales on the Bering Strait, Alaska. This variety, like *R. gelidus* and *R. kamchaticus,* is of interest for its occurrence both in Siberia and on the American side of the Bering Sea. *R. gelidus* extends from the Altai Range in Central Siberia across the Bering Sea Region to the Brooks Range and thence intermittently down the Rocky Mountain System to Colorado. The other two species follow portions of this track, *R. glacialis* var. *Chamissonis* from Siberia to the Brooks Range and *R. kamchaticus* from the Altai region to the Bering Strait region (Teller, Alaska). All three and particularly *R. kamchaticus* are small, obscure species, and they may turn out to have longer North American distributional ranges than are known now.

Var. *Chamissonis* and *R. gelidus* follow the northern mountains of Alaska and not the southern ones, which offer evidently equally favorable alpine habitats. In the Pleistocene Epoch large areas in southern Alaska and Canada were under four successive ice sheets, but the eastern side of Bering Strait, the Arctic Coast, and the Brooks Range were not. These species evidently have survived the glaciations in a northern Alaskan refugium beyond the ice sheets. Their occurrence on both sides of Bering Strait indicates possible survival since the last land connection across the Bering Sea at least as far back as Pleistocene time.

Specimen examined.—BROOKS RANGE (NORTH SIDE). "Sandstone rubble on ridge top, Thunder Mountain, northeast side, scarce," 68° 40′ N 160° 20′ W, *Spetzman* 4443 (MIN).

Subgenus BATRACHIUM (DC.) A. Gray (Treatise:229)

11   RANUNCULUS AQUATILIS L. var. ERADICATUS Laestad. (Treatise:239)

Circumpolar. Umiat, 400 feet, Colville River, northernmost foothills of the Brooks Range; south side of the Brooks Range at 3,000 feet and descending lower into the spruce forest.

This wide-ranging variety occurs in boreal regions around the northern hemisphere. Its evident absence from the Arctic Coast and from the higher areas on the north side of the Brooks Range indicates that it is not a high northern plant but one mostly of the southern fringes of Arctic Regions, as is true of *R. Flammula* var. *filiformis,* collected also at Umiat and on the south side of the Brooks Range. Both occur also in the spruce forests for some distance southward.

Specimens examined.—BROOKS RANGE (NORTH SIDE). Umiat, Colville River, 69° 30′ N 152° W, *Spetzman* 2631 (MIN), *H. J. Thompson* 1307 (DS, POM).

BROOKS RANGE (SOUTH SIDE). Nolan, *Jordal* 2344 (MICH); summit 15 miles north of Wiseman, *Jordal* 2268 (MICH); Arctic Village, *Jordal* 3621 (MICH).

Subgenus PALLASIANTHA L. Benson (Treatise:246)

12 RANUNCULUS PALLASH Schlecht. (Treatise: 256; Suppl. : 369)

Perhaps circumpolar, but the Old World distribution not fully determined. Common along the Arctic Coast; north side of the Brooks Range up to 2,300 feet elevation.

This species was observed in the small ponds on the tundra in the vicinity of Point Barrow, where it imparts a reddish color to the zone in which it grows in the cold water underlain a foot to twenty inches below the surface by permafrost. In mid-August, 1950, most plants were in flower, but in one pond they were fruiting.

Specimens examined.—ARCTIC COAST. Cape Lisburne, *Mason* in 1931 (UC); east end of Pearl Bay, *Black* in 1947 (US); Ooglamie, *Murdock* in 1883 (GH); "Pt. Barrow," *Murdock* in 1883 (GH, US), *Seale* in 1896 (DS, CAS), *McIlhenny* 47 in 1898 (NY, CAS, RM); Barrow, *J. P. Anderson* 4311 (ISC); Pt. Barrow, 71° 21′ N 156° 40′ W, *Spetzman* 2388 (MIN); 1 mile inland from Will Rogers Monument, 15 miles southwest of Barrow Base, *Wiggins* 12461 (DS, POM); 1½ miles south southwest of Barrow Base, *L. Benson* 14525 (POM, US), and 5 sheets to be distributed; 1½ miles south of Barrow Base, *Wiggins* 12522 (DS, POM); 4 miles south of Barrow Base, *J. H. Thomas* 2156 (DS, POM); 7½ miles south of Barrow Base, *J. H. Thomas* 2049 (DS, POM); 11½ miles south of Barrow Base, *L. Benson* 14589 (POM, US); Iko Bay 71° 12′ N 156° 2′ W, *J. H. Thomas* 2211 (DS, POM); Alaktak, Half-Moon 3, 70° 45 N 155° W, *Spetzman* 2467 (MIN).

BROOKS RANGE (NORTH SIDE). Lake Noluk (scarce), 68° 47′ N 160° W, *Spetzman* 4264 (MIN); Umiat, Colville River, 69° 30′ N 152° W, *Spetzman* 2206 (MIN); Sadlerochit River, 69° 30′ N 145° W, *Spetzman* 1105 (MIN).

Subgenus COPTIDIUM (Nym.) L. Benson (Treatise:247)

13 RANUNCULUS LAPPONICUS L. (Treatise: 247; Suppl. : 369)

Circumpolar in the southern portion of the arctic region and in the northern spruce and fir forests. Approaching the Arctic Coast at Alaktak, 50 feet elevation; north side of the Brooks Range up to 2,300 feet; south side at about the same elevation or a little higher.

Specimens examined.—ARCTIC COASTAL REGION. Alaktak, Half-Moon 3, 70° 45′ N 155° W, *Spetzman* 2521 (MIN).

BROOKS RANGE (NORTH SIDE). 1 mile west of Lake Noluk, 68° 47′ N 160° W, *Spetzman* 4299 (MIN); Lake Noluk, *Spetzman* 3910 (MIN); Nimiuktuk River, 68° 20′ N 159° 55′ W, *Spetzman* 3546 (MIN); Colville River, 68° 52′ N 156° 18′ W, *Spetzman* 2248 (MIN); Maybe Creek, 69° 20′ N 154° 30′ W, *Spetzman* 2622 (MIN); Umiat, Colville River, 69° 30′ N 152° W, *Spetzman* 1290 (MIN), 2138 (MIN); Sadlerochit River, 69° 30′ N, 145° W, *Spetzman* 1135 (MIN).

BROOKS RANGE (SOUTH SIDE). South of Wiseman, *Jordal* 2190 (MICH).

Notes and Discussion

Castanea dentata and Staphylea trifolia in the
Indiana Dunes State Park

In my article showing "A List of the Trees and Shrubs of the Indiana Dunes State Park" (Amer. Midl. Nat. 49:904-907, 1953), I stated that *Castanea dentata* and *Staphylea trifolia* had become extinct in the park. Mr. Terzo P. Amidei, park naturalist, has corrected me in this and has shown that both species still survive. There are numerous bladdernuts a short distance west of Tremont Road and south of the east fork of Dunes Creek, which attain a diameter of about 1⅛ inches. There is one sapling chestnut with a diameter of 3 inches and height of about 20 feet a few feet west of the east fork of Dunes Creek and a short distance northwest of the old colony. This tree is perfectly healthy and may have developed resistance against the Asiatic chestnut blight. These two species plus *Rosa blanda, Epigaea repens* and *Sambucus pubens calva*, shrubby species discovered since the list was published, make a total of 123 species of woody plants in the Indiana Dunes State Park.—KENDALL LAUGHLIN, 312 N. Central Ave. Chicago, Illinois.

Two Additions to the Amphibian Fauna of Burkes Garden, Virginia

The salamanders and frogs collected at Burkes Garden, Tazewell County, Virginia, have been the subject of a report published four years ago (Hoffman & Kleinpeter, 1948, Amer. Midl Nat. 39(3):602-607. To the list of 16 species then recorded may now be added two more, as a result of recent visits to the area. One of them is of considerable interest from a zoogeographic standpoint.

Pseudotriton ruber nitidus Dunn.—On June 28, 1952, I collected an adult female of this subspecies on the east side of Garden Mountain, on the road between Burkes Garden Post Office and Sharon Springs. This locality is in Bland County, but is certainly to be included in the Burkes Garden region. The specimen was found under a log in dry oak-hickory woods, at an elevation of about 3000 feet. It agrees with typical *nitidus* in the immaculate venter, discrete dorsal spots, and unspotted distal third of the tail.

So far as is known, *nitidus* is recorded only from two places in Virginia—White Top Mountain and Abingdon. The range is herewith extended some 40 miles to the northwest, into a completely different physiographic province (Ridge and Valley) from that to which *nitidus* has been considered confined (Southern Blue Ridge). A parallel is to be found in the case of *Plethodon jordani metcalfi* Brimley. It will be very interesting to see how the ranges of *nitidus* and *ruber* work out when adequate material from southwest Virginia is available (*e.g.*, the National Museum has a rather typical *ruber* from Wytheville, Va.). Probably some altitudinal vicariation will be involved.

Rana catesbeiana Shaw.—Numerous bullfrogs were heard in the millpond at Gose Mills, in the Garden, on June 23, 1950, by J. A. Fowler and me. This is, I suspect, the highest locality (3000′) at which the species is known in Virginia.

To be further noted is the collection, along with the *Pseudotriton*, of an additional specimen of *Eurycea bislineata*. This individual, an adult female, appears to be intermediate between *E. b. bislineata* and *E. b. wilderae*, but may be listed *pro tempore* under the latter name (*op. cit.* p. 606).

A conspicuous absentee from the roster is *Desmognathus quadramaculatus*, which has not yet been found around Burkes Garden, although occurring on both sides (Marion, Va.; Bluefield, W. Va.), and being the object of special search in recent years.

The Burkes Garden list now stands at 18 species—11 salamanders and 7 frogs. Of the former only 5 are common widespread forms; the remaining 6 are of particular note as regards distribution. It is hoped that a closer application of seasonal collecting will secure some more of the species which doubtless occur in the region, but which have so far escaped notice. I would mention especially *Diemyctylus, Ambystoma maculatum, Hemidactylium, Aneides*, and *Rana sylvatica*.—RICHARD L. HOFFMAN, Clifton Forge, Virginia.

PUBLICATIONS

BOREAL HEPATICAE
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Pp. vi+428, 110 plates

Paperbound, postpaid $4.00